

by Donald B. Miller

Biology of the Kaminuriak Population of barren-ground caribou Part 3



Environnement
Canada

Environnement
Canada

0016390J S

REPORT SERIES (CANADIAN WILDLIFE SERVICE)

7003978 H M

SK
471
C345
No. 36

Canadian
Wildlife
Service
Report Series
Number 36

Errata **Biology of the Kaminuriak Population of barren-ground caribou**

Part 3: Taiga winter range relationships and diet

by Donald R. Miller

Canadian Wildlife Service
Report Series Number 36

Page 16, Figure 4:

The figure originally printed should be replaced with the graph shown on the reverse side of this page.

Page 17, Table 8, heading for
third column from the left:

*For Mean *%*
*Read Mean *g*

Page 29, right column, second sentence:

For Cladina alpestris, on the other hand, is a less preferred reindeer forage in Scandinavia and northwestern Manitoba (Scotter, 1965c),....

Read Cladina alpestris, on the other hand, is considered questionable as a preferred forage in Scandinavia and northwestern Manitoba (Scotter, 1965c),....

Page 31, middle column, end of first sentence in last paragraph:

*For....*which was slightly less than Pegau (1968b) found on the Seward Peninsula in (*C. rangiferina*).

*Read....*which was slightly less than Pegau (1968b) found on the Seward Peninsula in Alaska at three locations, 4.3–5.8 (*C. alpestris*) and 5.0–5.8 (*C. rangiferina*).

Page 32, left column, first paragraph, end of first sentence:

For...., somewhat less than Beckel's estimate of 0.25 per cent for approximately the same area during the 20-year period 1935–66 (Table 16).

Read...., somewhat less than Beckel's estimate of 0.25 per cent for approximately the same area during the 20-year period 1935–55 (Table 16).

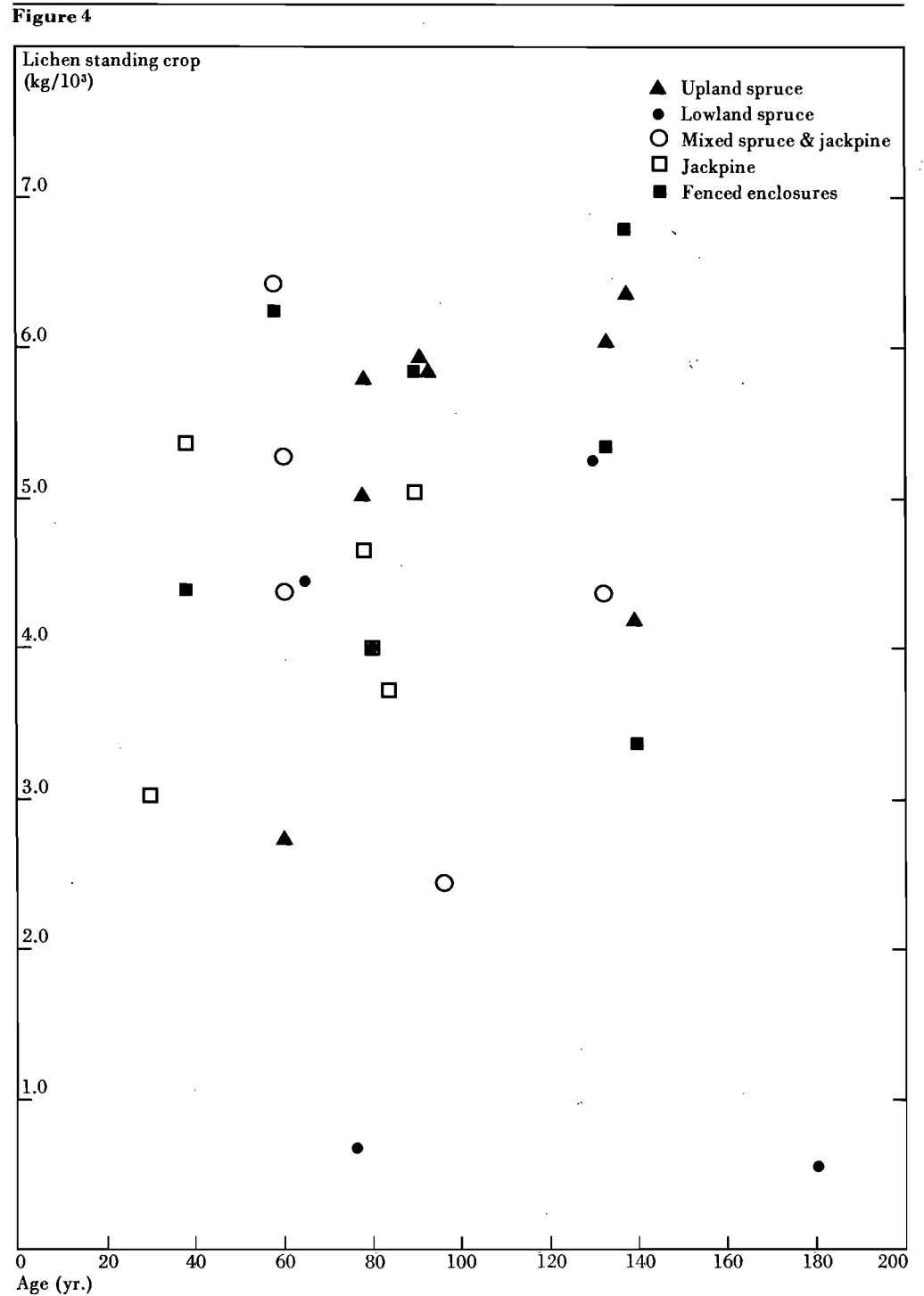
Page 32, left column, first paragraph, second sentence:

For In contrast, forest fires burned an estimated 0.87 per cent of land area annually from 1940 to 1955 on a study area in north-central Saskatchewan (Scotter, 1964).

Read In contrast, forest fires burned an estimated 0.87 per cent of land area annually from 1945 to 1959 on a study area in northcentral Saskatchewan (Scotter, 1964).



Figure 4
Lichen standing crop plotted against age of tree
stand on study sites





Environment Canada
Wildlife Service

Environnement Canada
Service de la Faune

Biology of the Kaminuriak Population of barren-ground caribou

Part 3: Taiga winter range relationships and diet

by Donald R. Miller

00163905 S
70139784 M

Canadian Wildlife Service
Report Series Number 36

A series to consist of four parts:

Part 1:

Total numbers, mortality, recruitment,
and seasonal distribution by G. R. Parker

Part 2:

Age and sex composition and segregation
of the population by F. L. Miller

Part 3:

Taiga winter range relationships and
diet by D. R. Miller

Part 4:

Growth, reproduction and nutritional
condition by T. C. Dauphiné, Jr.

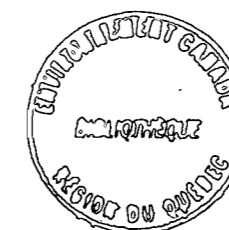
SK

471

C345

NO. 36

SCF



Issued under the authority of the
Minister of the Environment

Canadian Wildlife Service

© Crown Copyrights reserved
Available by mail from
Information Canada, Ottawa,
and at the following
Information Canada bookshops:

Halifax
1735 Barrington Street

Montreal
1182 St. Catherine Street West

Ottawa
171 Slater Street

Toronto
221 Yonge Street

Winnipeg
393 Portage Avenue

Vancouver
657 Granville Street

or through your bookseller
Price:
Canada \$1.75
Other countries \$2.10
Price subject to change without notice
Information Canada
Catalogue No. CW65-8/36
Ottawa, 1976

Design: Gottschalk+Ash Ltd.
Printing: D.W. Friesen & Sons Ltd.
Contract No. KL 131-5-9129

Cover: Caribou trail in mid winter to feeding site
in semi-open spruce, northwestern Manitoba.
Note the muzzle marks along the trail where car-
ibou searched for the scent of forage beneath
the snow.
Photo by Donald R. Miller

Contents

6	The author
6	Acknowledgements
6	Perspective
6	Abstract
6	Résumé
7	Russian abstract
7	Introduction
8	Study area
9	Study periods
10	Seasonal availability of vegetation
10	1. Methods
10	1.1. Aerial photography
10	1.2. Study plots
10	1.3. Lichen growth on caribou pellets
10	1.4. Standing crop and nutritional analyses
11	2. Results
11	2.1. Aerial photography and occurrence of fires
12	2.2. Vegetation on study plots
14	2.3. Lichen growth on caribou pellets
16	2.4. Standing crop and nutritional analyses
18	Forage utilization
18	1. Methods
18	1.1. Winter forage utilization
18	1.2. Feeding crater observations and enclosures
18	1.3. Rumen contents
19	2. Results
19	2.1. Winter forage utilization
19	2.2. Feeding crater observations and enclosures
23	2.3. Rumen contents
23	2.3.1. Locational changes
23	2.3.2. Seasonal changes
24	2.3.3. Forage selection on taiga

26	Physical environment
26	1. Methods
26	1.1. Climatic measurements
26	1.2. Soil analyses
26	2. Results
26	2.1. Climatic measurements
28	2.2. Soil analyses
28	Discussion
28	1. Snow
29	2. Food habits
31	3. Lichen growth
31	4. Forest fires
32	5. Condition of range
33	6. Capacity of taiga range
35	Summary
36	Literature cited
38	Appendices

List of tables	
11	Table 1. Proportions of major land and cover types on 12,106 km² of caribou winter range in northwestern Manitoba, as interpreted from coloured aerial photographs, June and July 1967
13	Table 2. The relative age, number, and size range of forest fires that occurred in a 12,106-km² area of northwestern Manitoba between 1955 and 1967 as determined from coloured aerial photographs
13	Table 3. Mean and range of density, size, and age of trees on study plots and enclosures
13	Table 4. Mean and range of cover estimates (%) of plants occurring on more than four study plots or enclosures
14	Table 5. Mean and range of percent-ages by weight of major lichen genera in study plots and enclosures
14	Table 6. Re-establishment of lichens on 1-m² plots during first 27 months after removal of lichens in June 1967
15	Table 7. Protein and energy values of forage plant samples taken in summer from 1-m² plots
17	Table 8. Estimation of standing crop of terrestrial lichens from cover measurements and weight of lichen divots

20	Table 9. Percentage frequency of heavily cratered sites among habitat types observed from the air in February 1967 and 1968
20	Table 10. Percentage frequency of forage items found in crater and arboreal forage collections in early, mid, and late winter, 1967–68
20	Table 11. Occurrence of lichens and vascular plants at caribou feeding sites used in mid and late winter, 1968, at Hara Lake, Saskatchewan
21	Table 12. Location, date established, size, and forest cover of crater enclosures
21	Table 13. Percentage intermediate and ground cover in the caribou crater enclosures at Hara Lake, Saskatchewan
23	Table 14. Percentage occurrence of plants in caribou rumen samples
25	Table 15. Seasonal comparison by weight of rumen contents
32	Table 16. Comparison of aerial photograph interpretations of samples of caribou winter range made in taiga of northern Saskatchewan and northwestern Manitoba

List of figures

8	Figure 1. Forest regions in the range of the Kaminuriak caribou population (after Rowe, 1959)
11	Figure 2. Proportions of major land and cover types of a 12,106-km ² area of caribou winter range in northwestern Manitoba as determined by air photo interpretation
12	Figure 3. Areas burnt by forest fires on 11,432 km ² of caribou range in northwestern Manitoba between 1955 and 1967, and areas with conifer reproduction less than 0.3 m high and between 0.3 and 1.8 m high in 1955 (after Beckel, 1958)
16	Figure 4. Lichen standing crop plotted against age of tree stand on study sites
24	Figure 5. Weight of the five major forage items found in caribou rumens collected in 1966–68
26	Figure 6. Daily range of temperatures recorded at sites within caribou range in the taiga during early, mid, and late winter periods, 1967–68
27	Figure 7. Range of snow depths and crust hardness measured in cover types during early, mid, and late winter periods, 1967–68
30	Figure 8. A comparison of percentage occurrence of the four most common lichen genera

List of appendices

38	Appendix 1. Forest type, location, topography, density, size, and age of trees in study plots and enclosures
39	Appendix 2. Percentage cover of plant species occurring in more than four study plots or enclosures
40	Appendix 3. Mean and range of percentages by weight of major lichen genera in study plots and enclosures
41	Appendix 4. Location and forage plant cover of square metre plots established in 1967

The author recording vegetation data from an area cratered by caribou in early winter. The area had been marked with a tripod of poles while snow remained on the ground. It was remarked with spray paint (not obviously visible in this photo, see outline) in summer for future reference. Photo by K. E. Hungerford.



Dedication

To Horace Macallum, Cree, trapper, woodsman, companion and gentleman.

The author

Donald R. Miller obtained an M.Sc. in 1957 from Pennsylvania State University. He spent 3½ years as Central District Biologist in Newfoundland doing research on beaver. In 1961 he joined the Manitoba Wildlife Division to study fur-bearers and, 2 years later, began work on big game in northern Manitoba. In 1966 he joined the Canadian Wildlife Service (CWS) in Ottawa to take part in the Kaminuriak barren-ground caribou study. In 1976 he completes his Ph.D. work at the University of Idaho. His dissertation deals with wild-fire and barren-ground caribou.

Acknowledgements

I thank my co-workers: T. C. Dauphiné, Jr., F. L. Miller, G. R. Parker, and G. Tessier. E. Brodo, R. Ireland, and W. Baldwin, all of the National Museum of Canada, identified the lichens, mosses, and vascular plants, respectively. W. Cody, Canada Department of Agriculture, identified vascular plants. J. Looman, A. Johnston, and A. McLean, Canada Department of Agriculture, and J. Lambert, Carleton University, advised in sampling vegetation. Logistic help was received from O. Blackburn, Department of Indian and Northern Affairs; G. Johnstone and W. Meade, Manitoba Department of Mines, Resources and Environmental Management; and R. Hunter, Manitoba Government Air Service. P. Hislop, Chief of the Brochet Indian Band, kindly located assistants for field work. Thanks are due to the following field assistants; H. Macallum, T. Dettanikkeaze, N. Dantlouse, A. Merasty, P. Bigheddy, and L. Denegaz of Brochet, and especially to H. Saunders of York Landing. I am grateful to K. Miller for identifying plant fragments in rumen samples and other assistance throughout the study. I am particularly thankful to D. Flook and A. Gunn for suggesting improvements to the manuscript.

Perspective

Barren-ground caribou in northern Canada numbered about three million in primitive times. The introduction of firearms to the native people, the arrival of whalers in the mid-19th century, and the demand for northern furs in the early 20th century all contributed to an increase in the annual kill of caribou. The caribou population declined locally as early as the mid 1800s and range-wide after 1900. By 1948-49 aerial surveys showed only an estimated 670,000 caribou. The decrease continued until 1955 when numbers stabilized. During that time caribou studies monitored the decline and identified some of the factors responsible. The need for more comprehensive information and the concern of several conservation agencies led the CWS to initiate an intensive study of caribou in 1966. The study lasted 2½ years and centered on the Kaminuriak Population, an accessible population with a relatively confined range. The study was in four parts: total numbers, mortality, recruitment and seasonal distribution; sex and age composition; seasonal physical and reproductive condition; and winter range evaluation. A CWS biologist was responsible for each section, but the game agencies of Manitoba, Saskatchewan, Alberta, and Northwest Territories (NWT) all contributed personnel at various stages.

Abstract

The winter range of barren-ground caribou in northwestern Manitoba was studied to learn what potential forage was available, and how weather, in particular snow conditions, affected the foraging of caribou.

The potential forage was determined from standing crop and percentage cover of green plants and lichens in study plots. Feeding caribou were observed, and plants were collected from feeding craters and enclosures. Further evidence and confirmation of observed feeding habits were obtained by an analysis of rumen contents.

The results of climatic measurements, especially of snow depth and crust hard-

ness, explained the sudden changes observed in caribou diet. The diet changed from predominantly terrestrial lichens and grass-like plants in early winter to arboreal lichens and woody browse in late winter when the snow crust prevented caribou from digging craters. As the snow thawed the caribou fed heavily on exposed plants and lichens especially along the spring migration routes. Otherwise there was no evidence that the caribou were exerting pressure on their winter range forage. Aerial photographs, evidence of rates of lichen recovery, and knowledge of feeding habits allowed some general conclusions to be drawn about the capability of the winter range to support caribou. In particular forest fires are beneficial in that they increase the heterogeneity of the plant cover and favour the growth of some lichens which occur in early successional stages. There is a plentiful supply of forage in the area despite caribou use and fires. Snow cover rather than scarcity of forage limits the capacity of the taiga to support caribou.

Résumé

On a étudié l'habitat hivernal du caribou des toundras dans le nord-ouest du Manitoba pour en déterminer les disponibilités de pâture et comment les conditions météorologiques, la neige surtout, pouvaient influencer sur le régime alimentaire de cet animal.

Les disponibilités fourragères ont été déterminées à partir du peuplement sur pied et du pourcentage de couverture du sol par les plantes vertes et les lichens en parcelles d'observation. On a observé les caribous en pâture, et on a recueilli des plantes dans les entonnoirs et cuvettes où ils se nourrissent. L'analyse du contenu du rumen a apporté d'autres renseignements qui ont confirmé les observations de ses habitudes alimentaires que nous avons effectuées sur le terrain.

Les données climatologiques, notamment l'épaisseur de la neige et la dureté de la croûte de surface, ont permis d'expliquer les variations brusques constatées dans le

régime alimentaire du caribou. Composé surtout de lichens terrestres et de plantes herbacées au début de l'hiver, le régime comportait, à la fin, des lichens arboricoles et des ramilles quand la croûte de neige empêchait le caribou de creuser des entonnoirs. À la fonte des neiges, les caribous faisaient grande consommation des végétaux et lichens exposés, surtout le long des voies de migration printanière. Rien d'autre n'indique que les caribous exercent une pression sur leurs pâturages d'hiver. Les photographies aériennes, des indices sur les taux de repousse des lichens et la connaissance des habitudes alimentaires du caribou ont permis de tirer certaines conclusions générales sur les possibilités fourragères de ses pâturages d'hiver. Les feux de forêts en particulier le servent en rendant la végétation plus hétérogène et en favorisant la croissance de certains lichens qui apparaissent aux stades initiaux de la régénération de la sylvie. La région ne manque pas de pâture malgré tant l'emploi qu'en fait le caribou que les feux. C'est l'enneigement plutôt que la rareté des ressources fourragères qui limite la capacité qu'a la taiga d'entretenir le caribou.

Абстракт

Проводились исследования зимних пастбищ карibu на бесплодных землях северо-западной Манитобы с целью нахождения кормовой базы, а также изучение влияния погоды, в частности, снежного периода, на питание карibu.

В качестве кормовой базы были приняты растения на корню и частично зеленые растения и лишайники на изучаемых участках. Проводились наблюдения за карibu, принимающих пищу, собирались растения из лунок и оград, предназначенных для кормления. Дальнейшие подтверждения наблюдаемых навыков питания были получены в результате исследования содержимого рубца.

Климатические изменения, в основном глубина снежного покрова и твердость корки, объяснили неожидан-

ные изменения в питании карibu. Питание карibu, состоявшее раньше из наземных лишайников и травянистых растений в период ранней зимы, стало содержать древесные лишайники и молодые побеги поздней зимой, когда снежная корка не позволяла карibu рыть углубления с целью нахождения пищи. По мере таяния снежного покрова карibu питались преимущественно обнаженными растениями и лишайниками, особенно по дороге во время весенней миграции. Не было свидетельства усиленного отыскивания корма на зимнем пастбище. Аэросъемки, наличие свидетельства о восстановлении лишайников и знание привычек кормежки карibu позволили сделать некоторые общие заключения о способности зимнего пастбища пропитать карibu. Лесные пожары особенно благоприятны в этом отношении, так как они увеличивают разнородность растительного покрова и способствуют росту лишайников, которые появляются в ранних последовательных стадиях. В таких районах, несмотря на пожары, карibu находят изобилие корма. Основным фактором, ограничивающим способность тайги пропитать карibu, является не недостаток корма, а наличие снежного покрова.

Caribou winter on the taiga, the far northern boreal forest. Winter range is a possible factor limiting caribou populations and forest fires have reduced its capacity to support caribou. Therefore CWS included a study of the winter range in their intensive investigation of the biology of the Kaminuriak Population. The objectives of the study were to appraise the amount and quality of vegetation on the winter range, to relate seasonal changes in caribou food habits to availability, to estimate capacity of the taiga to sustain current use, and to collect data on the physical environment especially snow conditions. Since caribou use the taiga only during winter, I separated the food habits study into four periods according to snow characteristics: early winter, a period of snow accumulation and no major restrictions to caribou movements; mid winter, a period of continued snow accumulation and major restrictions to caribou movements by deep and wind-crusted snow; late winter, a period when the snow forms a hard crust because of alternating freezing and thawing; and spring, when snow crusts deteriorate and depths decrease. I included information on forage use on the tundra and the ecotone between tundra and taiga to give the reader a more complete picture of the caribou's food habits.

Study area

The study area was the part of the taiga inhabited by caribou of the Kaminuriak Population during the study. I did all vegetation studies in northwestern Manitoba, except for analyses of some crater sites in northeast Saskatchewan.

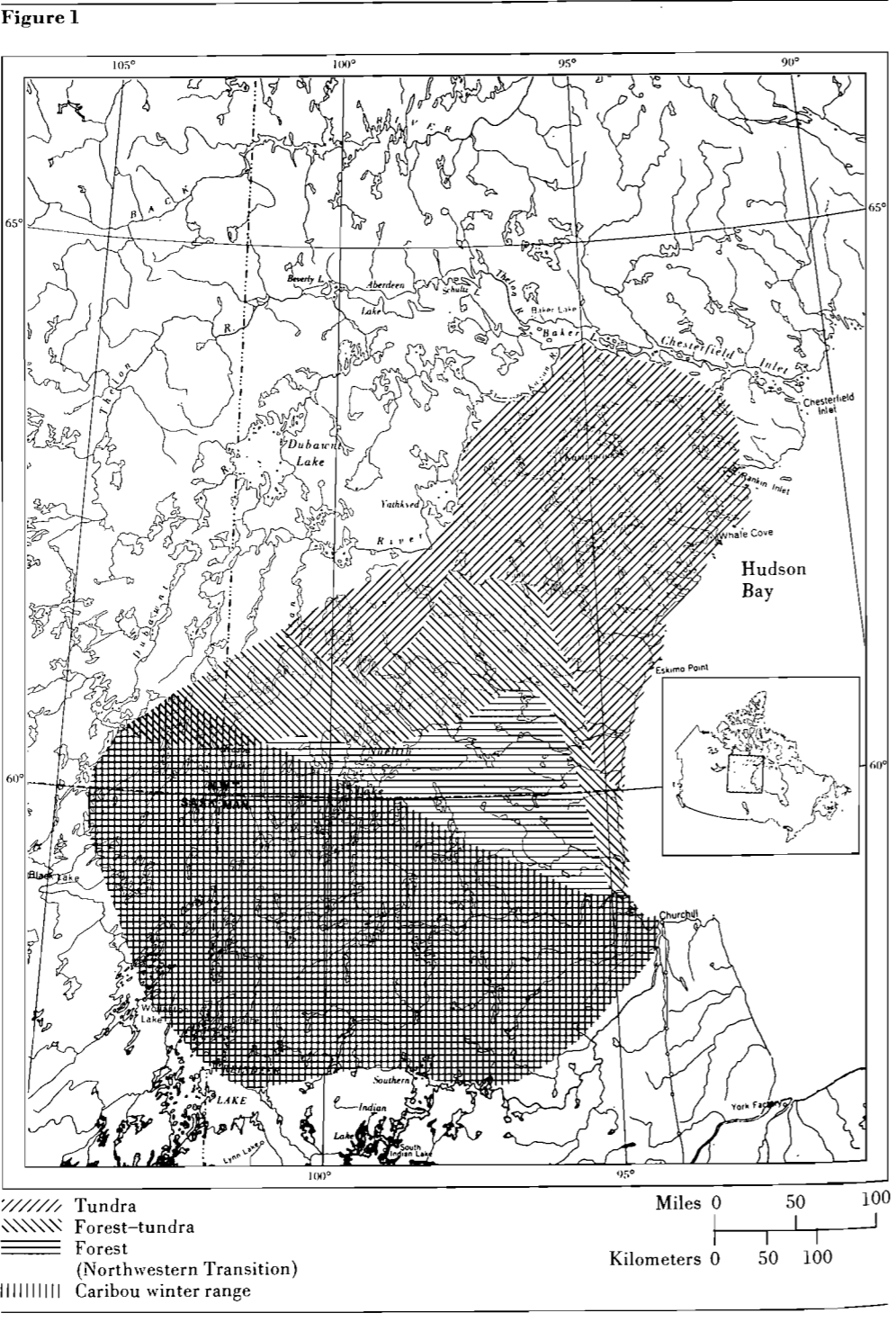
The winter range of the Kaminuriak Population, according to tagged caribou returns (Miller and Robertson, 1967) lies almost completely in forest (called the Northwestern Transition Section by Rowe, 1959). A small portion of the winter range extends northwest into the Forest-Tundra Section, a transition zone between the subarctic forest and tundra (Fig. 1).

The landscape is patterned with all the forms of glacially moulded drift overlying Precambrian granites and gneisses. The two major land forms (Ritchie, 1962) are patternless and drumlinized drift plains. In patternless drift plains the relief is low and rolling with extensive bogs between drumlins, rock outcrops and major moraines. In drumlinized drift plains the relief is moderate with extensive elongated bogs and occasional fens in the depressions between ridges.

Soils are mainly fine and coarse sand. Podzols are common on the better drained sites. The main portion of the area lies within the discontinuous permafrost region with the northwest corner in the region of continuous permafrost (Brown, 1960).

The vegetation is a mosaic of forest muskeg and fen cut across by sandy eskers and areas of open water. The most abundant tree is black spruce (*Picea mariana*). Jack pine (*Pinus banksiana*) is abundant on upland sites in the southern part of the range. White spruce (*Picea glauca*) grows on the favourable soils of eskers and sand plains. White birch (*Betula papyrifera*) is often found in association with spruce and pine on dry sites, and tamarack (*Larix laricina*) with spruce on wet sites. White aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) are uncommon, growing only on sheltered sites. Willows (*Salix* spp.), dwarf birch (*Betula* spp.),

Figure 1
Forest regions in the range of the Kaminuriak caribou population (after Rowe, 1959)



Study periods

alder (*Alnus crispa*), scattered white birch, and tamarack border the lakes and streams.

Dominating the shrub vegetation on upland sites are the ericoid shrubs *Vaccinium vitis-idaea*, *V. uliginosum*, and *Ledum groenlandicum* in the north, and *V. myrtilloides* in the south. *Chamaedaphne calyculata*, *Kalmia polifolia*, and *Andromeda polifolia* are common in wet sites. In the fens, along lake and stream shores are *Calamagrostis canadensis*, *Carex* spp., and *Scirpus* spp., with *Eriophorum* spp., *Juncus* spp., and *Equisetum fluviatile* locally abundant.

Ground cover on many upland sites is made up of dense lichen mats. The major lichen species at these sites in the drumlinized drift plains, according to Scotter (1965a), are *Cladonia mitis*, *Cladonia rangiferina*, *Cladonia alpestris*, *Cladonia amaurocrea*, and *Cladonia uncialis*. *Cladonia gracilis* can be added to this list in the patternless drift plains. The feather mosses, principally *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium* spp., *Dicranum* spp., and *Polytrichum* spp. are common in the ground cover of the better drained sites along with the liverwort *Ptilidium ciliare*. *Sphagnum* spp. dominate the mosses on wet sites.

Winters are long and severe, and summers are short, dry, and cool. Annual precipitation is about 38 cm and falls mainly in the warmest months, July and August. Minimum precipitation occurs in February. The total snowfall is about 152 cm, and the period with the largest accumulation on the ground is in February and March.

I did field work in all seasons except freeze-up and break-up. I observed food habits, weather, and snow during early, mid, and late winter and spring, from 1966 to 1968. In early summer, I assessed condition of sites used as feeding craters during the previous winter and measured tree cover and lichen standing crop. I measured and collected vascular plants and observed recovery of plants on disturbed sites at the end of summer. I made a preliminary field trip in mid summer 1966 to test various methods of sampling vegetation and to become familiar with the habitat and signs of caribou winter activities.

Seasonal availability of vegetation

I surveyed the winter forage to assess the types and areas of habitats, and the distribution, quantity, and quality of the potential forage within the habitat types.

1. Methods

1.1. Aerial photography

An area of 12,106 km² was photographed in colour from the air during late June and July 1967 at an altitude of about 2,743 m. Scale of the photographs was 1:15,840.

The area photographed included the entire Whiskey Jack Lake Topographic Map Sheet 64K of NTS 1:250,000 Series, published in 1962 by the Surveys and Mapping Branch, Department of Mines and Technical Surveys, Ottawa. The same area had been photographed in black-and-white during July and August 1955 at a scale of 1:60,000, and the plant cover of 11,432 km² had been interpreted and mapped (Beckel, 1958).

M. R. Robinson interpreted the coloured aerial photographs. He marked the following habitat types with India ink on one of the stereo pairs:

- Sparse spruce
- Dense spruce
- Sparse jack pine
- Treed swamp (birch draws)
- Meadows (fens)
- Recent burn
- Water
- Miscellaneous
 - Boulder fields
 - Small islands of mixed habitat
 - Cabin community sites

Minimum size of any one habitat type marked was 2 acres and a dot grid overlay was used to determine acreages at a rate of one dot equals 0.5 acres.

1.2. Study plots

I selected sites for vegetational studies in four areas of traditional caribou winter range in northwestern Manitoba. Crown canopy and drainage conditions served as a basis for categorizing cover types. I allotted the number of sites in each

cover type on the basis of its comparative abundance as follows:

Upland spruce	8 study sites
Lowland spruce	6 study sites
Jack pine	6 study sites
Spruce and jack pine	5 study sites

I sampled the vegetation of each study site in a 5 x 25 m plot, called the macroplot. No more than 10 m from each macroplot I marked a second plot of the same size on contour with the first plot. Both plots were marked with stakes. I removed no vegetation from the second plot but left it undisturbed for future reference.

In both the macroplot and the replicate, I counted trees taller than 2 m. I measured height and diameter at breast height (d.b.h) of five large trees in or adjacent to the two macroplots and determined age of the stand by taking core samples from two or more dominant trees at about 30 cm above the ground. I cut down occasional trees and determined the age of the butts using a hand lens.

Within each macroplot I sampled the intermediate and ground cover from 20 1-m² microplots selected at random. I estimated the cover with the use of a frame (Daubenmire, 1959), 20 x 50 cm, placed in the lower left-hand corner of each microplot. The canopy coverage of each species was estimated according to six classes: less than 5, 5 to 25, 25 to 50, 50 to 75, 75 to 95, and more than 95 per cent. The total cover can exceed 100 per cent by this method because some plants grow over the tops of others, as for example, lichens covering mosses.

I measured relative abundance and standing crops of lichens in a dm² divot sample selected from within the lichen portion of ground cover in each of the 20 microplots. I estimated cover of each of the lichen genera, *Cladina*, *Cladonia*, *Stereocaulon*, *Cetraria*, and *Peltigira*, according to four classes — less than 25, 25 to 50, 50 to 75, and more than 75 per cent and the cover of individual species according to six classes — less than 1, 1 to 4, 5 to 9, 10 to 24, 25 to 49, and more than 50 per cent.

I counted mushrooms systematically in each macroplot during late summer.

I also sampled in 1967, six fenced enclosures, which had been constructed at two widely separated areas of caribou winter range in northwestern Manitoba during 1964 and 1965 (Engen, 1964 and 1965). I staked a macroplot within each of the 1,012-m² enclosures as at the study sites, and I sampled it similarly except that I extracted 10 instead of 20 divot samples, and collected no soil samples. I selected one study site adjacent to each enclosure, and used the soil samples and tree cover measurements from it to represent both the fenced and unfenced sites.

I observed plant recovery on 25 1-m² plots from which I had removed plants for measurement of standing crop and nutritional analysis. I established nine of the plots near to, but not within, macroplots on study sites. Six plots represented the lichen forage found at the enclosures, and 10 plots represented specific sites or lichen communities. I photographed the plots in colour and black-and-white after removing the plants. I estimated plant recovery visually and photographed it during subsequent observations.

1.3. Lichen growth on caribou pellets

In June 1967 I marked 18 caribou pellet (feces) groups from the previous winter in the vicinity of caribou enclosure No. 4 at Lac Brochet and transported one group inside the enclosure. I examined the pellets again in September 1968 and 1969.

1.4. Standing crop and nutritional analysis

I used dm² divot samples (as described above, 20 in each unfenced macroplot and 10 in each enclosure) to estimate standing crop of terrestrial lichens. I transported each divot sample to the laboratory and separated each into lichen and non-lichen components. I air-dried and weighed the lichen.

I hand picked samples of forage species for chemical analyses and measurement

Table 1 Proportions of major land and cover types of 12,106 km² of caribou winter range in northwestern Manitoba*, as interpreted from coloured aerial photographs, June and July 1967

		Extent of land or cover type, as per cent of total									
		Lowland			Spruce		Upland		Recent burn	Water	
		Muskeg	Birch draw	Meadow	Sparse	Dense	Sparse	Dense			
Portion of region mapped	Total area (hectares)										
Northwest quarter	311,400	24	1	7	30	3	3	1	7	24	
Northeast quarter	267,710	23	1	6	36	3	2	2	9	18	
Southwest quarter	318,849	26	1	5	28	1	13	2	4	20	
Southeast quarter	312,716	38	Tr	7	33	Tr	6	Tr	2	14	
Entire region	1,210,675	28	Tr	6	32	2	6	2	5	19	

* Map sheet 64K (Whiskey Jack Lake), Canadian topographical maps 1:250,000 series. Department of Energy, Mines and Resources.

of standing crop from 25 1-m² plots described in "Study plots," and partially air-dried them in the field. In the laboratory, foreign material was removed and air-dried and the pure samples weighed. A 100-gram subsample from each 1-m² plot supporting over 100 g of pure sample was analysed for energy and protein.

The samples were ground, air-dried, and analysed using a calorimeter to determine energy, and micro-Kjeldahl technique for nitrogen content. The same techniques were used on additional samples of *Cladina alpestris* and *C. rangiferina* collected from dense stands and divided into living and non-living components for separate energy and nitrogen analyses.

2. Results

2.1. Aerial photography and occurrence of fires

Interpretation of coloured stereo-photographs of 12,106 km² in northwestern Manitoba showed that the area is comprised of about 20 per cent water and 80 per cent land. The land surface includes about equal proportions of upland, with 80 per cent spruce and 20 per cent jack pine, and lowland, with 80 per cent muskeg and 20 per cent meadow (fen in Scandinavian and Russian literature) (Fig. 2). The upland is dominated by semi-open to open canopy and a

Figure 2 Proportions of major land and cover types of a 12,106-km² area of caribou winter range in northwestern Manitoba as determined by air photo interpretation

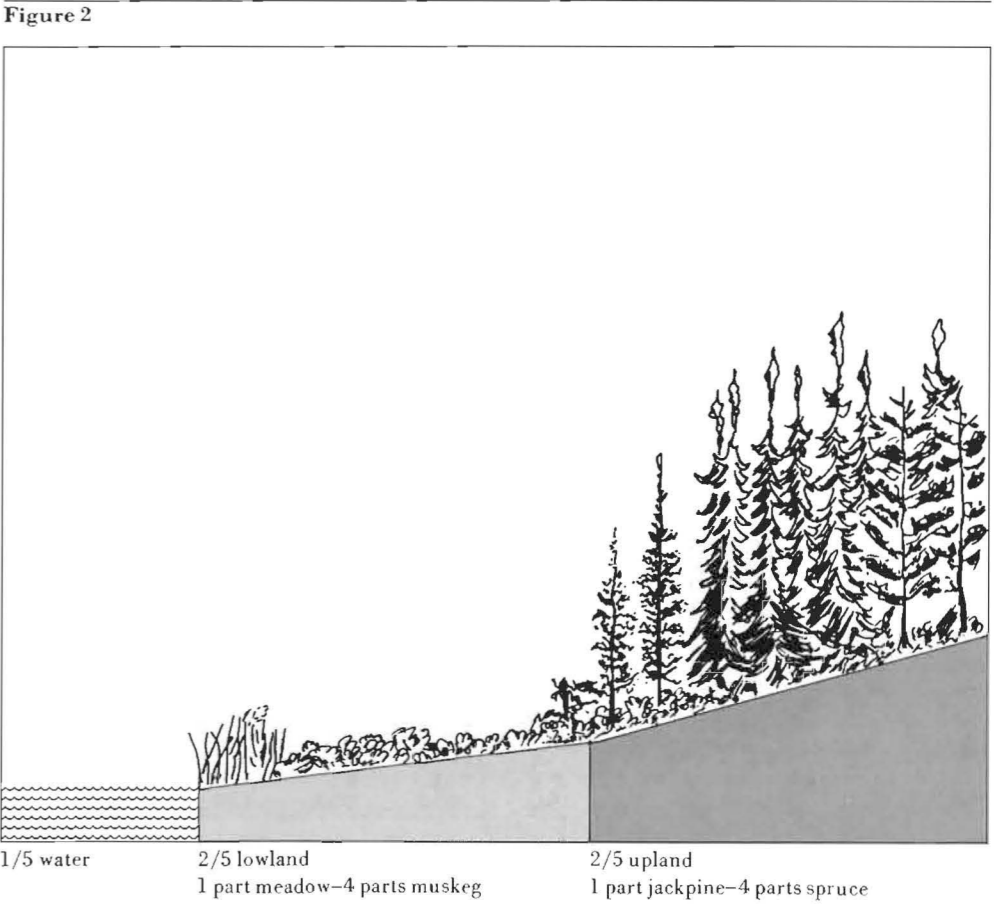
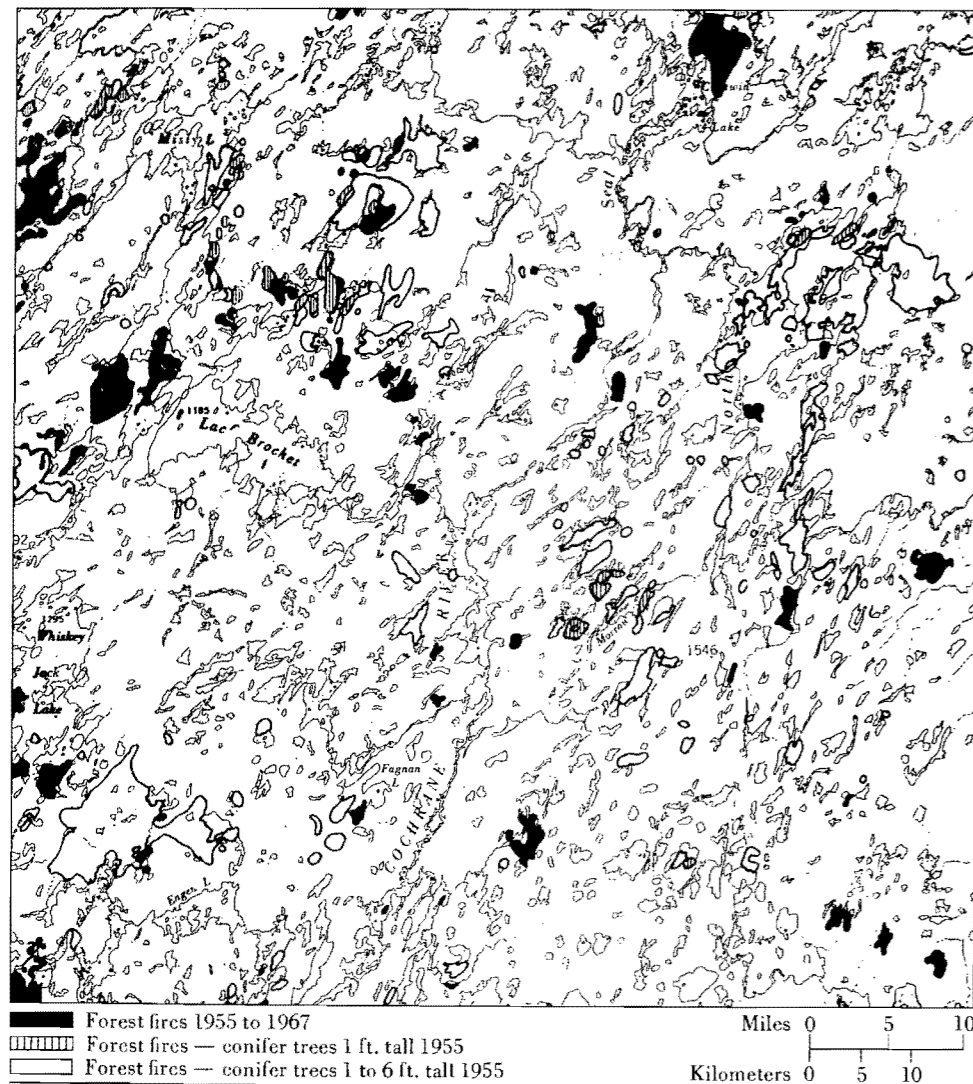


Figure 3



The proportions of landform and cover vary in different parts of the area mapped (Table 1). In the northwest there is a greater area of water — large streams and lakes. In the southeast is the greatest land area including much muskeg whereas in the southwest upland jack pine stands dominate the landscape. The number of jack pine

Based on Beckel's (1958) and my photographic interpretations of a 11,432-km² area, 47 fires from 1955 to 1967 (Fig. 3) had burned 2.1 per cent of the 9,200-km² land area. Thus, approximately 0.2 per cent of the land area, on average, had burned per year during the 12-year period, which,

I attempted to distinguish between recent, old and intermediate-aged burns that had occurred between 1955 and 1967, and to assess changes in the frequency of fires in the area (Table 2). Although it is not safe to assume that the three categories represented equal periods of time, the figures do not indicate any major change in frequency or size of forest fires between 1955 and 1967. Forest fires burned over both lowland and upland regions, but from data for the southeast quarter of the photographed area, upland regions were burned more than lowland. Of the 8,047 ha that had burned since 1955 in that quarter, 5,619 ha were in upland regions.

Appendix 1 describes 25 plots and six enclosures on which I studied vegetation. The plots were located on sites representing the most common topographical types of the treed portion of the winter range. I did not sample muskegs, meadows, or birch draws.

Low woody plants were more abundant on spruce than jack pine sites and on lowland in contrast to upland sites (Table 4, Appendix 2). I found *Vaccinium vitis-idaea* on all study sites: it has the greatest ecological amplitude of any vascular plant in the study area. *Ledum groenlandicum* and *L. decumbens* were abundant in spruce stands and especially on lowland sites.

Table 2

Relative age of area burnt	No. of burns	Size range, ha	Total area burnt, ha
Most recent (No green cover)	15	6-2,757	6,532
Recent (Partial green cover)	15	2-2,820	6,312
Old (Total green cover)	17	2-2,025	6,378
Total area burnt			19,222

Plot type	No. of plots	Trees per ha.	Height, m.	d.b.h., cm.	Age, yr.
Upland spruce	8	381 7-1,284	8.8 6.8-10.8	13.5 9.6-17.5	101 61-139
Lowland spruce	6	457 153-946	8.7 50-10	11.9 7.9-14.4	101 65-181
Mixed spruce and jack pine	5	218 89-422	10 10-10.4	15.7 10-20	81.2 58-132
Jack pine	6	425 160-709	8.2 6.0-9.9	10.6 6.8-14	66.6 30-90
Enclosures	6	563 89-1,285	8.6 6.0-10.8	12.7 9.1-17.0	98.6 38-139

Plot type	No. of plots	Lichens	Liver-worts	Mosses	Litter	<i>Vaccinium vitis-idaea</i>	<i>V. myrtilloides</i>	<i>V. uliginosum</i>	<i>Ledum groenlandicum</i>	<i>Empetrum nigrum</i>	<i>Geocaulon lividum</i>	Mushrooms (no. per ha.)	
						1967	1969						
Upland spruce	8	80.0	2.8	4.4	17.0	25.3	4.0	0.6	11.6	0.12	0	23.0	24.5
		58.92	0.5	0.20	10.34	12.33	0.20	0.4	0.54	0.1	0	0.64	0.86
Lowland spruce	6	56.5	2.5	31.8	19.3	26.8	0.6	4.3	18.5	0.8	0.3	82.8	72.2
		18.82	0.15	2.79	7.36	17.43	0.4	0.16	6.35	0.4	2	10.138	0.151
Mixed spruce and jack pine	5	74.8	1.0	2.4	22.4	29.4	7.2	6.0	1.4	0.2	0.2	51.4	98.3
		48.92	0.4	<1.5	10.40	5.50	2.12	0.26	0.6	0.1	<1.1	12.96	0.314
Jack pine	6	74.2	0.2	2.8	39.3	20.8	5.2	0	0.5	1.5	0.5	65.5	63.3
		62.88	0.1	0.7	22.69	1.39	0.12	0	0.3	0.4	1.2	20.131	0.235
Enclosures	6	80.6	2.2	3.5	30.0	14.7	5.3	1.8	3.1	<1	0	31.7	18.0
		70.86	0.5	0.15	9.43	0.35	0.20	0.10	0.8	0. <1	0	0.37	0.69

Table 5
Mean and range of percentages by weight of major lichen genera in study plots and enclosures

Plot type	No. of plots	<i>Cladina</i>	<i>Cladonia</i>	<i>Stereocaulon</i>	<i>Cetraria</i>	<i>Peltigera</i>
Upland spruce	7*	78.4 48-90	16.6 3-43	1.1 0-8	4.7 0-9	0.0 0.0
Lowland spruce	6	57.5 42-85	25.5 10-58	0.0 0.0	1.2 0-37	5.5 0-33
Mixed spruce and jack pine	5	76.6 70-90	18.4 7-28	0.4 0-2	4.6 0-12	0.0 0
Jack pine	6	70.7 53-93	25.7 5-42	1.6 0-10	2.0 0-5	0.0 0.0
Enclosures	6	77.3 60-90	17.2 8-28	0.0 0.0	5.5 0-19	0.0 0.0

* Divot samples were not collected from Plot 8.

Table 6
Re-establishment of lichens on 1-m² plots during the first 27 months after complete removal of lichens in June 1967

Metre plot no.	Lichen cover before removal	% cover of primary thalli June 1968	% cover of primary thalli Sept. 1969	% cover of secondary thalli Sept. 1969
1	<i>Cladina alpestris</i>	15	50	Tr
2	<i>Stereocaulon</i> spp.	50	75	50
3	<i>Cladina rangiferina</i>	10	10-15	Tr
4	<i>Cetraria nivalis</i>	20	50	10
5	Mixed spp.	10	50	Tr
6	Mixed spp.	5	10	0
7	<i>Stereocaulon</i> spp.	5	10	0
8*	Mixed spp.	0	2	0
9	Mixed spp.	5	50	Tr
12	Mixed spp.	10	25	0
13	Mixed spp.	5	25	Tr
14	<i>Cladonia</i> and <i>Cladina</i> spp.	10	10	Tr
16	<i>Cladonia</i> and <i>Cladina</i> spp.	0	15	Tr
17	<i>Cladonia</i> and <i>Cladina</i> spp.	0	25	0
18	<i>Cladonia</i> and <i>Cladina</i> spp.	0	25	Tr

* Two inches of turf and mineral soil removed.

pendix 2). Litter, including needles, twigs, and cones, was present on all plots and particularly abundant on the jack pine sites.

The branched *Cladina* species — often called reindeer lichens — were dominant. *Cladina mitis*, a lichen of early successional stages, was the most frequent and abundant lichen species. *Cladina alpestris* and *Cladina rangiferina*, both climax species, ranked second and third in abundance.

Cladonia uncialis, often associated with *Cladina mitis*, was common but sparse. *Cladonia gracilis*, a cup and horn species, and the foliose *Cetraria* were similarly frequent but not abundant. *Stereocaulon* and *Peltigera* species were generally uncommon though locally abundant (Table 5, Appendix 3).

Mushrooms were found on all study plots and enclosures in 1967 and all except four plots in 1969 (Table 4). The lowest

densities of mushrooms were found on dry spruce sites and some of the spruce-jack pine sites. Most mushrooms observed were small (< 5 cm).

Lichen regeneration on denuded 1-m² plots began during the first summer with inconspicuous primary thalli growing in small, scattered groups. After three summers, secondary thalli (podetia) appeared in 10 of 15 plots (Table 6). The most rapid lichen recovery occurred on plots with a deep humus layer and in semi-open to dense coniferous cover, where there was protection from wind and midday sun. Lichen podetia were not observed on Plots 6 and 7 which were on exposed sites with shallow humus layers. Lichen primary thalli grew on Plot 8 after three summers although the turf and upper layer of mineral soil had been removed. That plot was well protected from direct rays of the afternoon sun and from strong winds.

Re-establishment of vascular plants on defoliated plots varied by species and according to the material removed. On Plots 11A and 11B *Vaccinium vitis-idaea* recovered rapidly after three summers although *Empetrum nigrum* showed no recovery. *Ledum groenlandicum* grew rapidly after two summers when only the leaves had been removed, but where the stems were removed as well, recovery was slow. Removal of *Ledum* stems, however, appeared to cause a response in the growth of the lichens *Cladina rangiferina*, *Cladina mitis* and *Cladina alpestris* which grew sparsely under the dense *Ledum* cover.

2.3. Lichen growth on caribou pellets

In September 1968, two summers after the pellets has been deposited, they had disappeared on sites where *Stereocaulon paschale* was the dominant lichen, but were still conspicuous where *Cladonia* spp., *Cladina* spp. and *Cetraria nivalis* were dominant. On *Stereocaulon* sites the pellets had filtered down to the base of the podetia and were covered over by the upper parts. In both lichen communities the pellets had

Cladina alpestris growing in ball-like clumps at Brochet, Manitoba, where caribou utilization has not occurred for more than half a century. The author has observed this growth form only among the crevices of boulder fields within the utilized area of the taiga winter range.



Table 7
Protein and energy values of forage plant samples taken in summer from 1-m² plots. Protein is calculated by multiplying total nitrogen by 6.25. Dates given in appendix 4.

Plot no.	Forage type	Protein, %	Energy, k cal./100 g
1	Lichen, 75% <i>Cladina alpestris</i>	2.04	434
2	Lichen, 95% <i>Stereocaulon paschale</i>	10.16	480
3	Lichen, 50% <i>Cladina rangiferina</i>	2.00	425
4	Lichen, 50% <i>Cetraria nivalis</i>	2.54	426
5	Lichen, mixed	3.99	454
6	Lichen, mixed	2.92	416
7	Lichen, 75% <i>Stereocaulon paschale</i>	6.42	455
9	Lichen, mixed <i>Cladonia</i> and <i>Cetraria</i>	2.71	431
10	<i>Ledum groenlandicum</i>	8.27	566
11A	<i>Vaccinium vitis-idaea</i>	5.77	509
11B	<i>Empetrum nigrum</i>	6.27	551
12	Lichen, mixed	2.82	433
13	Lichen, mixed	1.96	435
14	Lichen, mixed <i>Cladonia</i> and <i>Cladina</i>	2.24	431
16	Lichen, mixed	2.60	437
17	Lichen, mixed	2.10	428
18	Lichen, mixed	2.12	434
20	<i>Carex aquatilis</i>	6.54	463
21	<i>Carex aquatilis</i>	5.25	452
22	<i>Equisetum fluviatile</i>	13.71	383
23	<i>Ledum groenlandicum</i>	8.36	569
25	<i>Equisetum fluviatile</i>	6.76	448
	* <i>Cetraria alpestris</i> live podetia	2.63	356
	dead podetia	1.82	345
	* <i>Cladina rangiferina</i> live podetia	4.14	366
	dead podetia	2.18	357

* Additional samples.

Arboreal lichens on a jack pine growing on an esker at Ducharme Lake, Manitoba.



Figure 4.
Lichen standing crop plotted against age of tree
stand on study sites

retained their shape but had become smaller and covered by small cracks.

In September 1969, when marked pellet groups were three summers old, they were no longer conspicuous in *Cladonia*, *Cladina*, and *Cetraria* lichen communities. On close examination the pellets were found, and on many, primary lichen thalli had covered up to 10 per cent of the pellet surface area. The thalli were on the area of the pellet that was protected from direct exposure. On one pellet a podetium of nearly 1 cm in length was growing among the primary thalli. I also observed primary thalli on the sheltered sides of moose pellets placed inside Enclosure No. 6, in June 1967, 3 years earlier. Evidently lichen regeneration is quite rapid on certain substrates in favourable environments.

2.4. Standing crop and nutritional analysis

Chemical analyses of sub-samples from 1-m² plots showed that the protein content of lichens ranged from 20 to 122 mg/g (means = 34 mg/g) and in vascular plants from 5 to 137 mg/g (mean = 68 mg/g). The two *Stereocaulon* lichen samples were especially high in protein (82.9 mg/g) and energy (467 kcal/100 g) as were autumn-collected samples of *Ledum groenlandicum* and *Equisetum fluviatile*. Protein content of samples of the latter species varied widely. This might be explained by different collection periods. For example, *Equisetum* Sample 22 with twice the protein content was collected before, and *Equisetum* Sample 25 after, a heavy frost and light snow cover. Appendix 4 shows the dates on which 1-m² plots were established, with locations and forage types.

The energy content of dead podetia of *Cladina alpestris* and *Cladina rangiferina* differed little from that of living podetia (Table 7), but protein content was lower in dead podetia.

Lichens at most plots appeared free of litter at first glance. However more than two-thirds by weight of the material removed from any single plot consisted of litter.

Figure 4

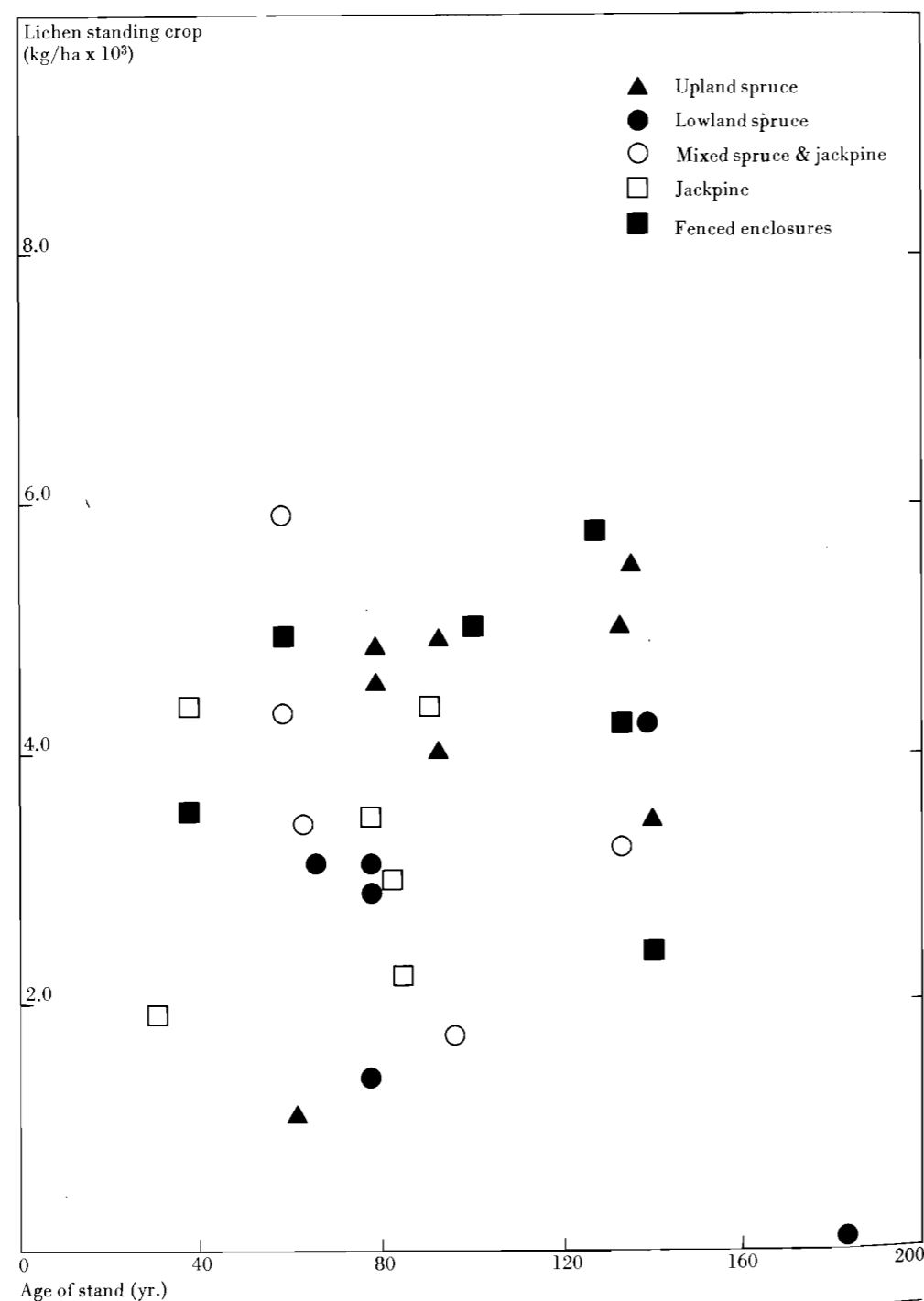


Table 8

Estimation of standing crop of terrestrial lichens
from cover measurements and weights of lichen divots

Plot		Mean* % lichen cover	Lichen material per dm ² -divot in lichen cover		Standing crop, † kg/ha
			Mean* %	SE	
1		92	5.47	0.55	5,032
2		81	7.30	0.60	5,913
3		86	7.42	0.37	6,381
4		81	5.18	0.40	4,196
5		84	7.21	0.58	6,056
6		79	7.54	0.70	5,957
7		80	7.28	0.51	5,824
8		59	4.65	0.39	2,744
9		70	6.35	0.55	4,445
10		21	3.37	0.50	708
11		18	3.11	0.50	560
12		82	6.39	0.53	5,240
13		79	5.08	0.42	4,013
14		70	5.79	0.52	4,053
15		48	5.16	0.68	2,477
16		81	6.53	0.45	5,289
17		76	5.77	0.79	4,385
18		77	5.70	0.32	4,389
19		92	7.00	0.44	6,440
20		62	6.03	0.46	3,739
21		72	5.66	0.35	4,075
22		79	5.88	0.34	4,645
23		64	4.71	0.43	3,014
24		88	5.74	0.37	5,051
25		80	6.72	0.37	5,376
Encl. 1	Jack pine	85	6.93	0.49	5,891
2	Jack pine	80	5.48	0.62	4,384
3	Mixed spruce and jack pine	79	7.86	0.69	6,209
4	Upland spruce	86	7.88	0.80	6,777
5	Upland spruce	70	4.80	0.51	3,360
6	Upland spruce	84	6.36	0.55	5,343

* Based on 20 macroplots, one divot in each, except in macroplots no. 6 and 7 and 11, in which numbers were 18, 19, and 16, respectively.

† Estimated by multiplying per cent lichen cover by mean weight of lichen material per dm²-divot from lichen cover and converting product to kg/ha

Caribou would ingest some litter along with lichens.

I found no relationship of the terrestrial lichen standing crop with age of the stand over 30 years. The local variation in standing crop and species composition of lichen stands could be at least partly associated with differences in slope, drainage, aspect, tree canopy, and past use by caribou. The relationship between lichen standing crop and age of the stand (Fig. 4) is possibly complicated by some or all of those factors. The standing crop of all but two study sites ranged from 2,000 to 7,000 kg/ha with the greater amounts from the dry spruce sites (Table 8). Two wet spruce sites supported less than 800 kg/ha.

Forage utilization

The previous section described the potential forage available to caribou in different habitats. The following section describes the forage on which the caribou were seen feeding or were known to have fed.

1. Methods

1.1. Winter forage utilization

I made aerial observations of heavily cratered sites during mid winter according to habitat:

Stream or lake shores	
Upland	densely treed sparsely treed to treeless
Lowland	densely treed sparsely treed to treeless open muskgs and meadows

I observed caribou feeding behaviour, feeding sites, and feeding period movements during all winter trips, using binoculars, a tripod-mounted telescope, and a flashlight, sometimes also a blind built of snow.

1.2. Feeding crater observations and enclosures

I examined fresh snow craters dug by foraging caribou and recorded the species occurrence of browsed plants. I also recorded signs of fresh browsing on tall shrubs, trees, and on arboreal lichens. I collected samples of browsed shrubs and grazed lichens, forbs, and grasslike plants¹ found in fresh craters. I followed many miles of caribou trails to collect feeding information.

I constructed 15 enclosures on cratered sites in winter and one in summer to observe the effects of caribou on forage during winter and the subsequent recovery of the plants. The enclosures, from 70 to 900 m², were in heavily cratered sites in treeless to densely treed types.

¹ Here and later in the text grasslike plants refers to: Equisetaceae, primarily *Equisetum fluviatile*; Graminae, primarily *Calamagrostis canadensis*; and Cyperaceae, primarily *Carex aquatilis*.



Within the enclosures I marked individual craters by a tripod of saplings tied together at the top. I used larger tripods of long poles to mark off areas that were not cratered. I tied a string around the trunks of trees on which lichens had been utilized. I made sketches of the enclosed areas and recorded locations of spots to be examined during the summer. I constructed three crater enclosures in January and February 1967 and 12 from November 1967 until May 1968.

I constructed one enclosure of woven wire mesh in September 1967 on a heavily grazed site, and I marked the boundaries of conspicuously grazed patches of lichens with blaze-orange paint. I also marked grazed sites outside the wire enclosure with stakes and paint to permit observation of the recovery of the grazed lichens, and sampled the vegetation inside the crater enclosures similarly to the permanent enclosures, with 10 randomly located micro-plots measured with the 20 x 50 dm frame (Daubenmire, 1959). The macroplot was 20 x 5 m instead of the 25 x 5 m sample in the permanent enclosure.

An intensively cratered site in sparse spruce in northern Manitoba. This is typical of mid winter cratering activity in deep soft snow

1.3. Rumen contents

Although the interpretation of analyses of rumen samples is complicated by the problem of differential digestion rates (Bergerud and Russell, 1964), rumen sampling provides quantitative information on food habits of wild ruminants.

I analysed rumen samples from 340 caribou shot in the study area for physiological and demographic study from 1966 to 1968. I analysed an additional 279 rumens from caribou shot on the tundra and ecotone between tundra and taiga during the same years.

I collected about one litre of rumen contents from each caribou, mixed it with either 10 per cent formalin solution or 95 per cent ethyl alcohol and transferred it to the laboratory. I shook the sample and took a 100-ml subsample which I washed, sieved, and sorted into the following categories: (1) mosses and liverworts, (2) twigs, (3) leaves, (4) grasses and grasslike plants, (5) conifer needles, (6) lichens, and (7) mushrooms. No more than 2 hours was allowed for the sorting after which the sample was air-dried, weighed, and preserved in 10

A fresh caribou trail leading to two *Larix laricina* trees heavily damaged by feeding activity on arboreal lichens



per cent alcohol. I discarded material unsorted after the 2-hour limit.

I repeated the analyses of two rumen samples, from each winter collection period, to check the consistency of the technique. I divided according to species, genus or broader group the samples of the broad categories: mosses and liverworts, leaves, grasslike plants, conifer needles, and lichens.

2. Results

2.1. Winter forage utilization

From aerial observations during February 1967 and 1968, upland, semi-open to open spruce stands appeared to be the sites most frequently used by feeding caribou during mid winter (Table 9). Lowland sites comprising muskgs, meadows, and grassy river and lake shores received more use in 1966-67 than in 1967-68. Caribou were in continuous movement northeast along drainage systems in 1966-67 and comparatively stationary in 1967-68.

In November-December 1967, migrating caribou were not restricted to the usual routes along water or eskers. Their

movements were not impeded by snow depth or crust. Caribou were observed feeding mainly at dawn and dusk on both upland and lowland sites and on lake and stream shores. They consistently fed during early winter in *Equisetum fluviatile* and *Carex aquatilis* communities on the shores of streams and lakes.

By February 1967, I observed caribou feeding less along lake and stream shores and more in semi-open upland spruce and jack pine stands, though along the Cochrane River they still fed extensively on *Equisetum fluviatile* and *Carex aquatilis*.

At Bonokowski Lake in northeastern Saskatchewan I saw feeding activity in upland, semi-open, white birch, and spruce stands and in lowland spruce sites where ericaceous plants and terrestrial lichens were abundant. I observed caribou feeding at midnight in late February at the shore of Bonokowski Lake and migrating in daylight or darkness. They migrated most consistently during the coldest periods.

In mid February 1968, caribou under observation at Hara Lake, Saskatchewan migrated steadily northward. They fed in

early morning and early evening though steady movements occurred anytime. Most feeding was on uplands in semi-open to dense spruce, and in white birch stands on islands. By the end of February, caribou had become stationary in the Hara Lake area, and daily feeding and resting periods became more regular. Caribou fed at similar sites as in mid February but I observed them resting on the lake ice more regularly and for longer intervals after early morning feeding periods.

In April the hardening of the snow crust from 2 months of trampling (Parker, 1972), and the effects of the sun and wind, caused a dramatic change in food habits. At Hara Lake, by mid April 1968, caribou fed almost exclusively on arboreal lichens and twigs of deciduous shrubs and trees, at midday as well as in early morning and evening.

By the end of April when the snow crust had softened, caribou no longer fed on arboreal lichens or browse. Instead they fed on terrestrial lichens and ericaceous plants that became available at thawed patches at the bases of trees, and on southern exposures of lake and stream banks, and eskers. Earlier in winter, caribou grazed repeatedly on the newly exposed foliage on southerly exposed slopes, cratered earlier in winter. As the snow receded with each day, feeding activities became more frequent and intense.

Only one animal fed in a crater at any time and caribou competed for certain crater sites. In early spring caribou fought with antlers and forefeet for preferred feeding sites.

2.2. Feeding crater observations and enclosures

The collection of plants from craters showed that grasses (*Calamagrostis*), sedges (*Carex*), and horsetails (*Equisetum*) were slightly more numerous than lichens at the feeding sites used in November and December (Table 10). As winter progressed lichens became the most common forage item. *Ledum* was the most common woody

Table 9
Percentage frequency of heavily cratered sites among habitat types observed from the air in February 1967 and 1968

	Upland sites				Lowland sites	
	Spruce, semi-open	Spruce, dense	Spruce and jack pine, semi-open	Jack pine, semi-open and dense	Open esker	Muskeg
1967*, n = 81	54	1	0	0	4	12
1968†, n = 203	57	4	8	1	4	16

* Brochet - Fort Hall Lake area.

† Brochet - Hara Lake area.

Table 10
Percentage frequency of forage items found in crater and arboreal forage collections in early, mid, and late winter, 1967-68

	Early winter November-December (n = 32)	Mid winter Feb. (n = 16)	Late winter April-May (n = 145)
Lichens	47	81	82
Arboreal	9	19	13
<i>Cladina</i>	34	56	61
<i>Cladonia</i>	22	38	42
<i>Stereocaulon</i>	16	31	30
<i>Cetraria</i>	34	31	26
<i>Peltigera</i> and <i>Nephroma</i>	0	0	4
Foliose	0	0	6
Grasslike plants*	50	19	14
Woody plants	9	25	24
<i>Lycopodium</i> spp.	0	6	2
<i>Myrica gale</i>	3	0	0
<i>Empetrum nigrum</i>	0	0	5
<i>Ledum</i> spp.	0	25	5
<i>Kalmia polifolia</i>	3	0	0
<i>Arctostaphylos uva-ursi</i>	0	0	3
<i>Vaccinium vitis-idaea</i>	3	13	23
<i>Vaccinium oxycoccus</i>	0	0	0

* Includes *Equisetum fluviatile*, *Calamagrostis canadensis*, and *Carex aquatilis*.

plant at sites used in February, and *Vaccinium vitis-idaea* at sites used in April and May.

Observations of craters and browsed trees and shrubs at Hara Lake, Saskatchewan from February to May agreed with the dramatic change observed in caribou feeding. In April-May arboreal lichens increased in importance while *Ledum*, *Vaccinium uliginosum*, and *Empetrum nigrum* were

less common in craters than they had been in February (Table 11). *Empetrum*, however, was utilized more by caribou in May when bare patches appeared in the snow cover.

In late February 1967 at Bonokowski Lake, Saskatchewan, the lichen, *Stereocaulon*, appeared to be equally as common in fresh caribou craters as *Cladina*, *Cladonia*, and *Cetraria*. However, no quantitative

Table 11
Occurrence of lichens and vascular plants at caribou feeding sites used in mid and late winter, 1968 at Hara Lake, Saskatchewan

	Occurrence, %	
	February 17-26*	April 23-28†
Terrestrial lichens	36	35
Arboreal lichens	0	46
<i>Ledum groenlandicum</i>	41	15
<i>Vaccinium uliginosum</i> ‡	10	2
<i>Chamaedaphne calyculata</i>	Tr	Tr
<i>Empetrum nigrum</i>	12	2
<i>Arctostaphylos uva-ursi</i>	Tr	Tr
<i>Lycopodium</i> spp.	Tr	0
<i>Salix</i> spp.	0	Tr

* 26 feeding sites, 541 craters.

† 20 feeding sites, 292 craters and 365 trees.

‡ *Vaccinium vitis-idaea* was not always recorded.

data were collected at that time. On April 27 and 28, 1968, at Hara Lake, a survey of craters revealed that *Stereocaulon* was present in 107 craters compared with *Cladina*, *Cladonia*, and *Cetraria* in 110 craters.

The enclosures built on cratered sites were in treeless to densely treed areas, the latter with trees aged from 35 to 129 years (Table 12). Most were in semi-open spruce, but one enclosure (No. 13) was constructed at a site in dense spruce where the caribou had fed extensively on arboreal lichens.

There was no apparent difference between February and April-May periods in either the intermediate or ground cover of sites used by caribou at Hara Lake, Saskatchewan (Table 13). *Vaccinium vitis-idaea*, *Ledum* spp., and *V. uliginosum*, in

Table 12
Location, date established, size, and forest cover of crater enclosures

No.	Location	Date established	Size, m ²	Forest cover type	Trees		
					Mean ht., m.	Mean d.b.h., cm.	Age, yr.
1	Cochrane River, Man.	1967 January	818	Jack pine, semi-open	9.6	12.9	84
2	Cochrane River, Man.	February	158	Lake shore	0	0	
3	Bonokowski Lake, Sask.	February	391	Spruce and white birch, open		8.9	97
4	Lac Brochet, Man.	September	65	Spruce, semi-open	10.1	14.5	129
5	Little Jackfish Lake, Man.	November	119	Spruce and white birch, open	10.2	18.8	73
6	Mihekun Lake, Man.	December	221	Spruce, semi-open	7.1	9.9	84
7	Lac Brochet, Man.	December	230	Spruce, open	6.1	10.4	35
8	Lac Brochet, Man.	December	90	Lake shore	0	0	
9	Hara Lake, Sask.	1968 February	225	Spruce, semi-open	8.9		69
10	Hara Lake, Sask.	February	250	Spruce, semi-open	10.7	15.7	122
11	Hara Lake, Sask.	February	253	Spruce, semi-open	8.5	10.9	116
12	Hara Lake, Sask.	February	100	Spruce, semi-open	7.9	15.0	52
13	Hara Lake, Sask.	April	215	Spruce, semi-open to dense	8.2	12.2	116
14	Hara Lake, Sask.	May	332	Spruce and white birch, semi-open	11.5	14.0	104
15	Hara Lake, Sask.	May	193	Spruce and white birch, open	4.9	8.1	49
16	Hara Lake, Sask.	May	293	Spruce, semi-open	6.6	10.2	70

order of importance, made up most of the intermediate cover, and lichens and mosses made up the living portion of the ground cover. I did not observe any exposed turf or mineral soil in the enclosures, but the ground cover included much wood and litter.

When I examined sites cratered in November-December in summer, evidence of grazing was barely recognizable. In February enclosures, lichen forage in individual craters showed some disarrangement and slight utilization. Stems of *Ledum groenlandicum* and *Vaccinium uliginosum*, in particular, showed signs of both trampling damage and browsing. In April before snow depths decreased and the crust melted, most intermediate and ground cover plants were protected from grazing and trampling. Corticolous lichens, tall shrubs, and deciduous trees were browsed extensively at that stage. However, when the snow crust softened in May there was an immediate return to terrestrial forage, and at snow-free sites used during that period the boundaries of the grazed sites were unmistakable.

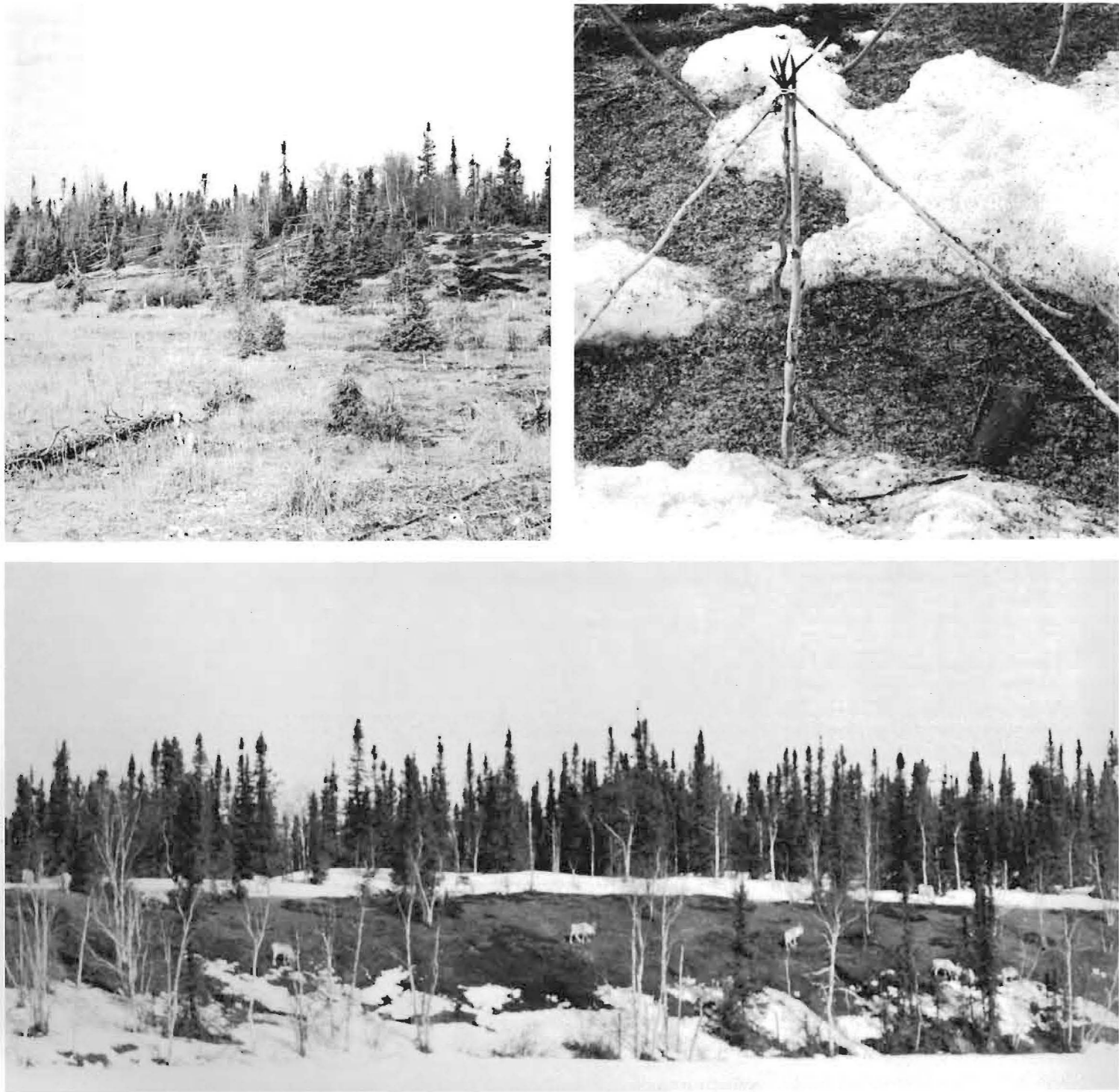
Table 13
Percentage intermediate and ground cover in the caribou crater enclosures at Hara Lake, Saskatchewan

	February				April			
	9	10	11	12	13	14	15	16
Intermediate cover								
<i>Equisetum</i>	0	0	0	0	Tr	0	0	0
Grasslike plants	0	0	0	0	0	0	0	Tr
<i>Geocaulon lividum</i>	0	0	Tr	0	0	0	0	0
<i>Empetrum nigrum</i>	2	0	42	0	2	0	0	17
<i>Ledum</i> spp.	10	10	Tr	27	33	35	28	3
<i>Kalmia polifolia</i>	0	0	0	0	Tr	0	0	Tr
<i>Vaccinium uliginosum</i>	3	50	8	0	0	42	0	50
<i>Vaccinium vitis-idaea</i>	65	50	4	33	42	50	8	20
Ground cover								
Lichen	42	27	77	25	52	58	33	73
Liverworts	0	0	2	0	0	2	0	0
Mosses	0	83	25	28	35	27	57	50
Wood and debris	42	25	33	65	42	42	35	50
Rock	2	0	0	0	0	17	0	0

Enclosure formed around area cratered by caribou in the winter, Hara Lake, Saskatchewan

Poles used to mark boundary of caribou crater inside enclosure at Hara Lake, Saskatchewan

Caribou feeding on exposed slopes



2.3. Rumen contents

I combined the plant species found in caribou rumens into forage classes. Table 14 shows rumen contents of caribou collected in the taiga.

Using chi-square tests, I found no differences in forage classes used between sexes or between cows in different reproductive conditions. I found few significant differences between locations within seasons. However forage utilized changed markedly according to the season.

2.3.1. Locational changes

Caribou were usually killed on lakes at several locations during each season (Miller, 1974). I found no significant difference ($P > 0.05$) in rumen contents between locations within seasons, except in June 1967, and April 1967 and 1968 ($P < 0.001$). Most caribou were shot while resting on lakes, and their immediately previous movements and feeding were unknown. However, some caribou were observed before being killed, and the feeding observations agreed closely with the rumen analyses. Rumen samples from nine caribou collected in January and February 1967, when they were migrating northward, suggested a shift during a 1-month period from a predominantly lichen diet on the lower Cochrane River, Manitoba to twigs and leaves at Bonokowski Lake, Saskatchewan. Grasslike plants were an important forage class in rumen samples collected in the Misty Lake area along the upper Cochrane River during early February.

2.3.2. Seasonal changes

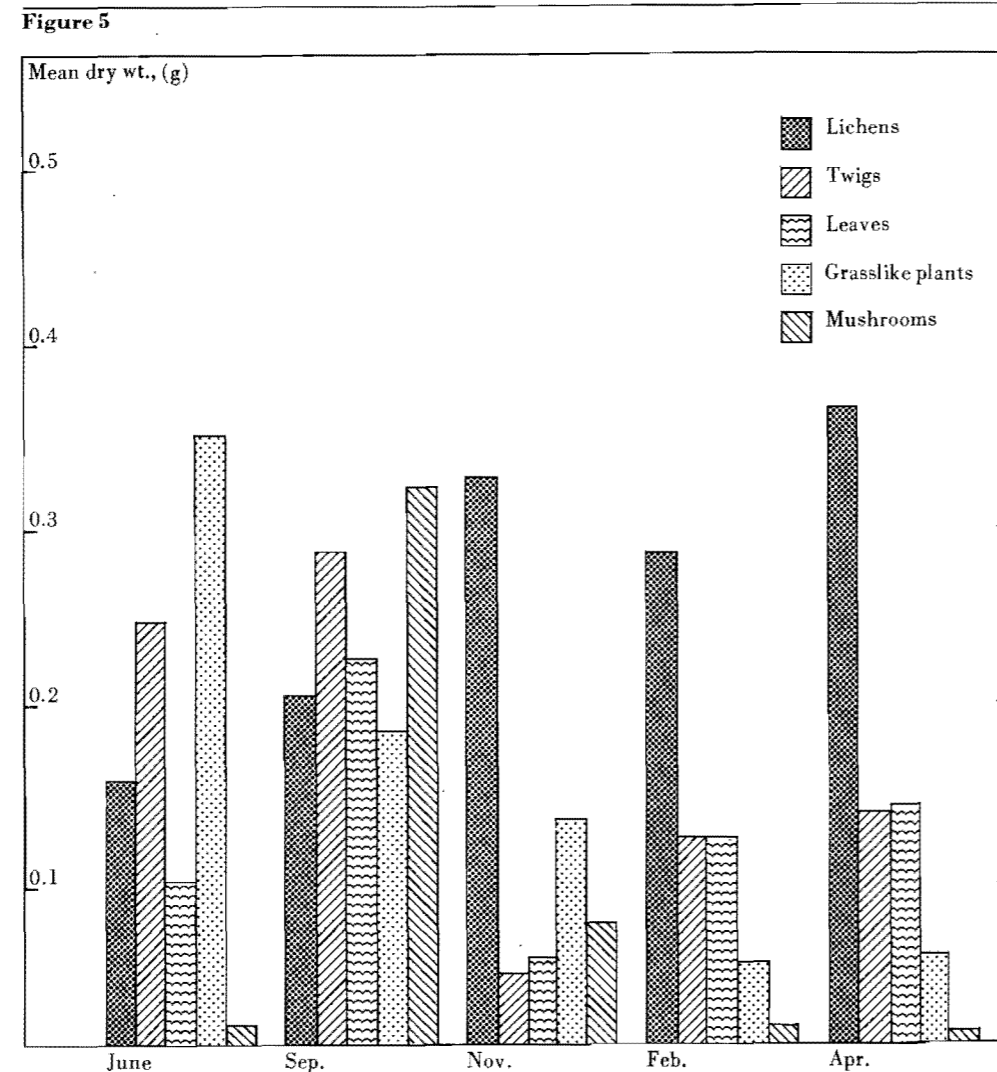
Analysis of 13 rumen samples collected in winter 1967-68 suggested that the caribou foraged on grasslike plants and lichens in early winter, and lichens and twigs and leaves of broad-leaved shrubs in mid and late winter, with lichens making up the major portion of the combined sample.

A seasonal comparison of the sample of 545 rumens (Table 15, Fig. 5) shows marked changes in proportions of the forage

Table 14
Percentage occurrence of plants in caribou rumen samples. Numbers in parentheses indicate numbers of rumens sampled

Plants	Collection period					
	Jan.-Feb.	April		November		
	1967	1966	1967	1968	1966	1967
Bryophyta	(14)	(19)	(20)	(20)	(20)	(20)
<i>Polytrichum commune</i>	43	21	40	10	45	25
<i>P. juniperum</i>	50	16	85	70	70	35
<i>P. piliferum</i>	36	0	66	20	55	20
<i>Dicranum</i> spp.	50	63	95	15	20	35
<i>Drepanocladus uncinatus</i>	14	0	25	5	0	5
<i>Pleurozium schreberi</i>	57	58	85	68	20	50
<i>Hylocomium splendens</i>	0	0	15	0	0	0
<i>Ptilidium ciliare</i>	64	84	100	75	25	50
Lichens	(7)	(26)	(80)	(72)	(85)	(57)
<i>Cladina</i> spp.	100	96	90	100	100	100
<i>Cladonia</i> spp.	43	65	20	54	62	42
<i>Stereocaulon</i> spp.	86	62	96	19	35	53
<i>Cetraria</i> spp.	0	0	0	0	4	0
Dead podetia	100	89	97	100	100	100
5% dead podetia	86	75	82	54	28	30
Conifer needles	(11)	(10)	(17)	(16)	(23)	(33)
<i>Larix laricina</i>	73	50	24	31	87	52
<i>Picea</i> spp.	100	100	100	100	78	100
<i>Pinus banksiana</i>	55	80	18	25	9	100
Woody angiosperms	(12)	(16)	(16)	(16)	(15)	(16)
<i>Salix</i> spp.	0	0	0	0	0	0
<i>Betula</i> spp.	17	19	63	50	13	38
<i>Rubus chamaemorus</i>	8	0	0	19	0	0
<i>Empetrum nigrum</i>	0	0	6	0	0	6
<i>Ledum</i> spp.	67	75	94	94	100	81
<i>Loiseleuria procumbans</i>	0	6	0	0	0	0
<i>Kalmia polifolia</i>	42	31	19	31	47	50
<i>Andromeda polifolia</i>	25	6	19	44	80	50
<i>Chamaedaphne calyculata</i>	0	6	0	50	40	6
<i>Arctostaphylos rubra</i>	0	6	0	0	0	0
<i>Vaccinium uliginosum</i>	92	81	75	19	67	81
<i>V. myrtilloides</i>	92	94	38	44	100	88
<i>V. vitis-idaea</i>	100	100	100	100	100	100
<i>Oxycoccus microcarpus</i>	0	0	6	0	20	0
Grasslike plants	(10)	(15)	(8)		(15)	(9)
<i>Equisetum</i> spp.	60	20	13		100	89

Figure 5
Weight of five major forage items found in caribou rumens collected in 1966-1968



Cladonia spp., although both genera occurred in most rumens. *Stereocaulon* spp. was a major component of the contents of some rumens collected in April.

Dead portions of lichen podetia occurred in most caribou rumen samples collected from the taiga, and half of the samples contained 5 per cent or more dead podetia (Table 14). The larger proportion of dead podetia in the April rumen samples, when compared to November, suggests that the caribou were either selecting forage dif-

ferently or feeding in different lichen communities in the 2 months. The primary lichen thallus was common in both November and April rumen collections.

Vaccinium vitis-idaea was the most common vascular plant eaten by caribou in the taiga in winter according to the occurrence of leaves in rumens (Table 14). *Ledum* spp., *Vaccinium uliginosum* and *V. myrtilloides* were also common in winter rumens. *Andromeda polifolia* and *Kalmia polifolia* occurred more commonly in ru-

Table 15
Seasonal comparison by weight of rumen contents

No. rumens	Period of collection	% of rumens in which forage class dominated			
		Twigs and leaves	Grasslike plants	Lichen	Mushrooms
126	November 1966-68	4	13	81	2
162	April 1966-68	43	4	52	1
132	June* 1966-68	42	47	11	
39	July 1968	77	23		
22	September 1966	27			73
64	September 1967	81	11	8	

* Rumens collected from 66°00'N to 65°00'N, 99°00'W to 100°00'W in June 1967 were different ($p < 0.001$); otherwise all locations combined.

mens collected in November and January-February than in those collected in April, suggesting that caribou fed more frequently in muskegs in early and mid winter. That was particularly evident when the relative abundance of the two plants in rumens was compared between the three winter seasons (Table 14).

Equisetum was found in some rumens collected in September, but was most common in November samples, and became progressively less common in the mid and late winter periods (Table 14). Jack pine needles appeared frequently in November rumens, the period when caribou were collected in the southern portion of the taiga winter range where jack pine stands are common. The occurrence of tamarack needles in rumens from the three winter periods suggests that caribou feed partly in lowland areas throughout winter. Tamarack is a common tree in the transition zone where the September 1966 caribou collections were made, and was the most common tree species represented in those rumens. Mosses occurred frequently in caribou rumens, either selected or accidentally eaten with other food. Eight moss species were identified in winter rumens and six were common in some seasons (Table 14). *Ptilidium ciliare*, however, was the only moss well represented during each collection period.

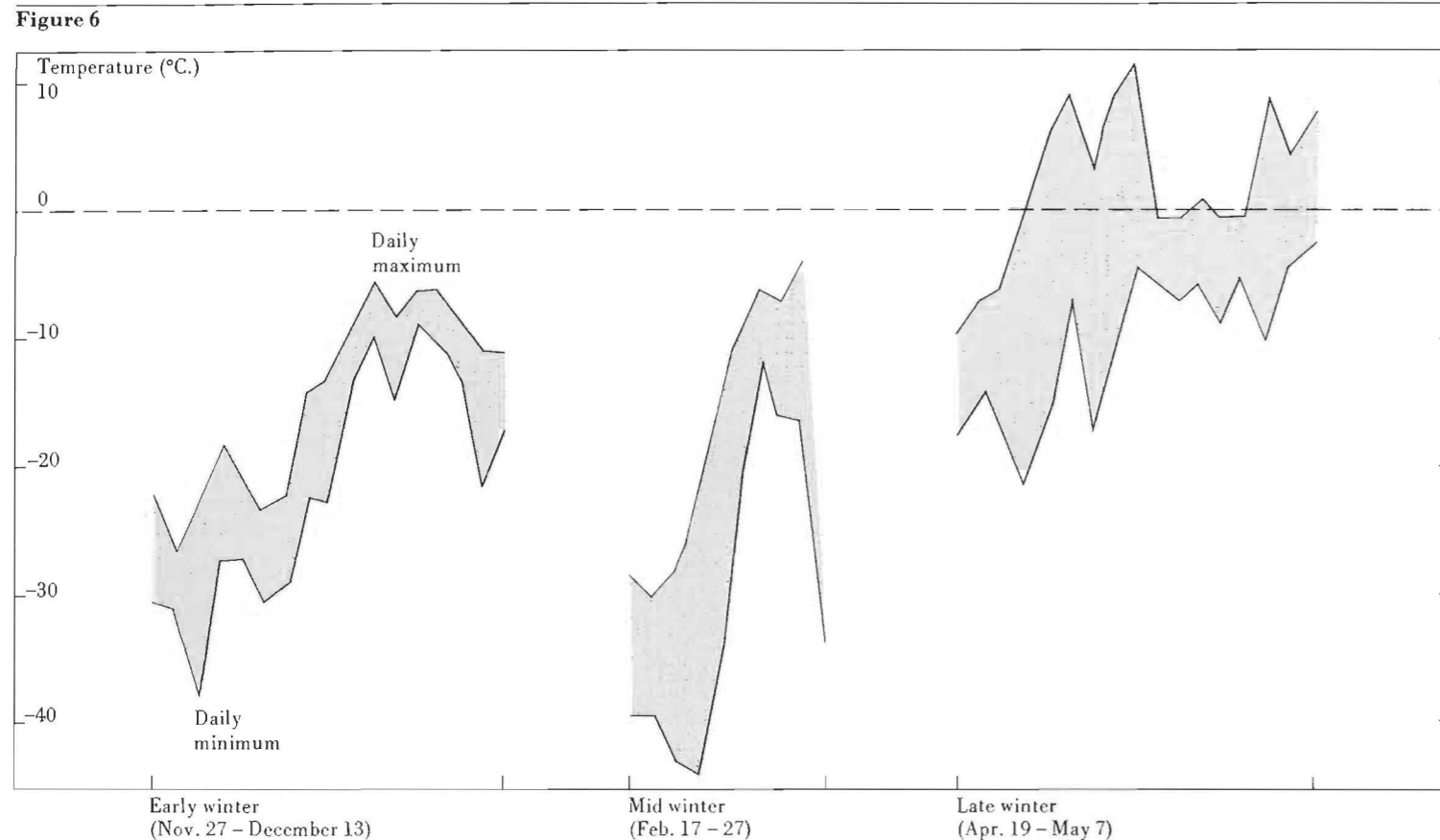
classes as the caribou moved through different habitat types. In the taiga lichens dominated the diet, especially in November. In April there was significantly ($P < 0.001$) less lichen in the rumens than in November, and a significant ($P < 0.001$) increase in twigs and leaves. In rumen samples collected in November grasslike plants were the second most abundant forage item, and that finding was supported by observations of grazing caribou. Although in April the proportion of grasslike plants had significantly ($P < 0.01$) decreased, by June they made up almost half the rumen contents. Dominance of lichen forage in rumens had significantly ($P < 0.001$) decreased from 80 per cent in November to about 50 per cent in April, dropping to about 10 per cent in June. The amounts of twigs and leaves were similar in April and June, but increased significantly ($P < 0.001$) in July, when they dominated the diet. Compared to June, about half as many July rumens were dominated by grasslike plants and none by lichens. In September the caribou fed in the forest-tundra zone, and their diet appears to have varied considerably depending on the availability of mushrooms. Between September 1966 and 1967, there were significantly different ($P < 0.001$) proportions of twigs and leaves and mushrooms.

The seasonal changes in the diet were modified by changes found between years. The rumen analyses suggest that caribou use woody plants and grass at about the same rate each year, but feeding on lichens and mushrooms may vary. Between April 1967 and 1968, there was a significant difference ($P < 0.001$) in use of lichens. During April, therefore, availability determines the use of lichens; in September the use of mushrooms depends on their availability.

2.3.3. Forage selection on taiga

Cladonia spp. and *Cladina* spp. far exceeded the occurrence and abundance of either *Stereocaulon* spp. or *Cetraria* spp. in the rumen samples collected from the taiga (Table 14). *Cladina* spp. made up a greater proportion of winter rumen contents than

Figure 6
Daily range of temperatures recorded at sites within caribou range in the taiga during early, mid, and late winter periods, 1967–1968



1. Methods

Measurements of the climate, in particular snow characteristics, helped to determine foraging patterns of the caribou.

1.1. Climatic measurements

I took climatic readings from 1966 to 1968 in the study area. I recorded temperatures from lake and coniferous forest sites using Taylor maximum–minimum thermometers. I placed the thermometers about 1 m above the snow surface. On lakes, I attached a thermometer to a spruce sapling anchored in snow at the edge of the wind shadow and, in forests, to the trunk of a spruce tree. The thermometers faced approximately north to prevent direct exposure to the midday sun. I recorded temperatures every morning and evening, and

during the day when weather changes were conspicuous. I used a Weston dialled soil thermometer with a 20-cm stem to record air temperatures away from camp and to measure temperatures below the snow over ground and lake ice, and periodically to check the accuracy of the maximum–minimum thermometers.

I estimated wind speed and direction each morning and evening at the same time as the temperatures were recorded. I checked estimates with an anemometer on one winter trip.

I measured undisturbed snow depths by probing at 10 or more points in each cover type and measured the hardness of snow crusts with an aluminum penetrometer designed and constructed by the National Research Council. That instrument

measures the pressure required, in pounds per square inch, for a disc of a known surface area to penetrate the crust. I used two discs, one for light and one for hard crusts.

1.2. Soil analysis

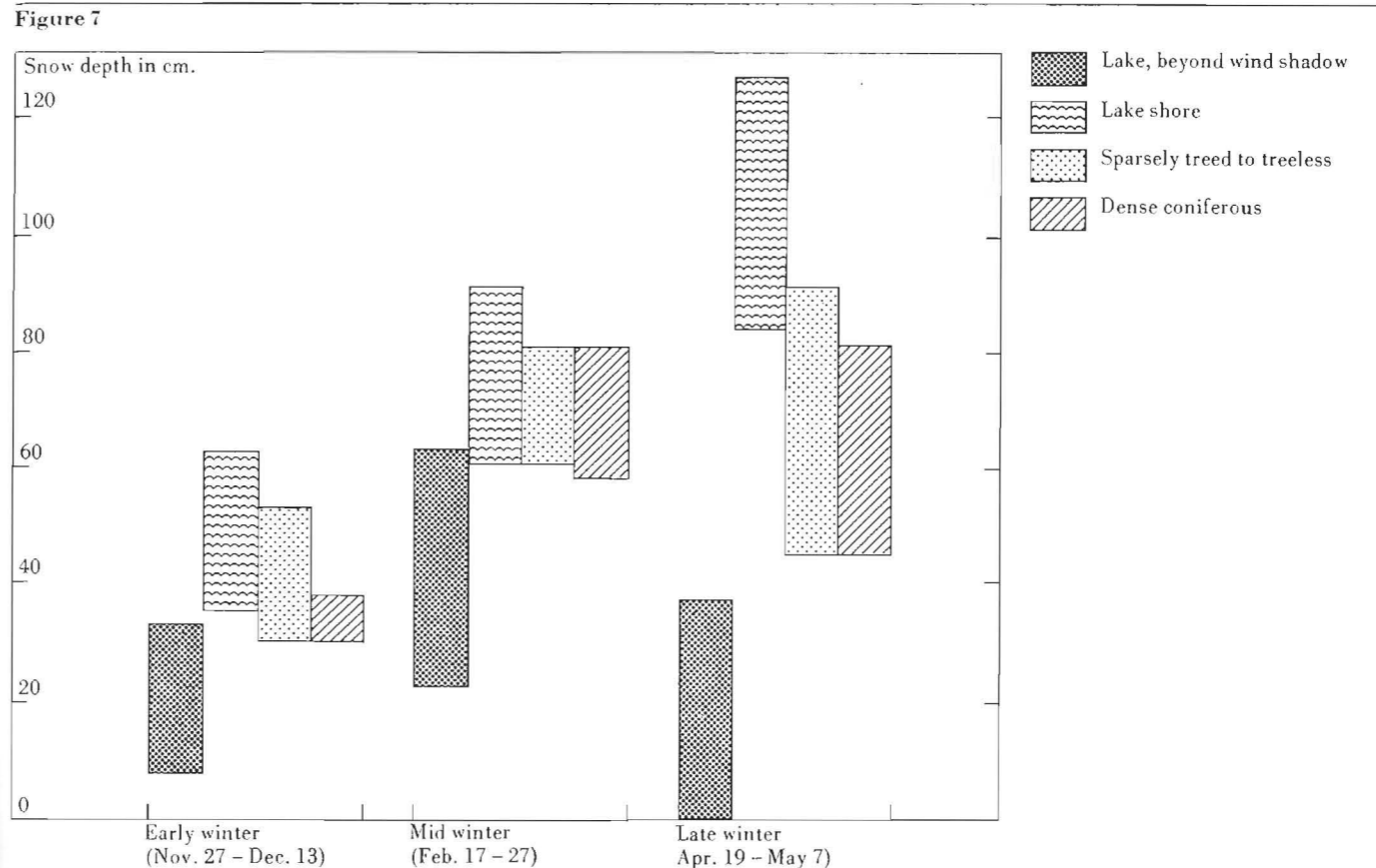
I collected soil samples from the study sites by extracting a plug from each corner and from the center of the macroplot. The Department of Soil Science at the University of Guelph analysed soils for texture and pH and for phosphorus, potassium, magnesium, and calcium content.

2. Results

2.1. Climatic measurements

The winter climate on the taiga varies from year to year, especially the mid winter climate. Between February 18 and 27, 1967,

Figure 7
Range of snow depths measured in cover types during early, mid, and late winter periods, 1967–1968



temperatures I recorded during field studies ranged between -43° and -19°C , and between the same dates in 1968, the temperature extremes were -43° and -4°C . On five days of the latter period the temperature rose above -18°C .

A comparison of daily temperature ranges for 1967–68 shows that greater temperature fluctuations, both within and between days, occurred in mid winter than in either early or late winter (Fig. 6). Temperatures rose above freezing on April 12, 1966, and April 24, 1968. The variation between years in the occurrence of above-freezing temperatures affects the timing of thawing of the snow surface.

The insulating effect of snow is important for the survival of forage plants. I recorded temperatures of -7 to -2°C be-

neath 66 to 71 cm of snow in January. *Equisetum fluviatile*, young, green sprouts of *Carex aquatilis*, lichens, and other forage plants beneath the snow surface are supple at such temperatures. Temperature of the lake ice surface under 50 cm of snow was -4°C in February when the ambient temperature was -32°C .

The snow was deepest on the lake shores, where drifts had accumulated among the first lines of trees and shrubs and in the lee of eskers.

In mid winter, 1967, the greatest snow depth recorded was 89 cm at a lake shore site, while on the same day depths on the open lake ranged from 35 to 53 cm and in semi-open conifer stands from 74 to 79 cm. In dense spruce stands the branches intercepted much of the snowfall in early

winter, resulting in smaller depths on the ground. Strong winds in mid winter dispersed the snow from the branches making depths on the ground in dense spruce similar to those of other habitats (Fig. 7). Prior to extensive thaws in late winter, the snow depth on lake and stream shores commonly reached 0.9 to 1.2 m. Snow depths in both semi-open and dense cover types remained similar to those recorded in mid winter, but on lakes a sharp decrease occurred by late winter.

Hard crusts appeared on lake snow by mid February 1968, as a result of wind. Large, rounded or razor-edged drifts formed on lakes during February creating an extremely uneven surface. The hard crust extended inland a short distance from lake and stream shores; in semi-open and dense

Discussion

conifer cover types the snow surface was only slightly harder than in early winter. But by late winter snow crusts on both open and semi-open sites were hard. Strong crusts developed on exposed sites when the sun melted the surface snow which froze in the evening. In addition, snow particles disturbed by daily feeding and movement of caribou fused together to form strong crusts. By mid April soft snow remained only in undisturbed, dense conifer sites. Crusts deteriorated rapidly by early May, breaking down first in the open sites, especially on southern exposures or eskers, hills, and steep banks of streams and lakes. Crusts formed during cold nights but thawed quickly on sunny days. Snow depths decreased rapidly in the open during that period, but slowly in semi-open and densely treed areas except around tree bases where the vegetation became exposed early.

Snow hardness was extremely important to caribou movement; it dictated the ease with which they could feed, migrate, and escape. Shallow, soft snow was no hindrance, but deep, soft snow impeded movements and excavation of craters. As a crust developed on the surface of deep snow caribou moved with increasing difficulty until it was strong enough to bear their weight. Juveniles were supported by snow with a crust strength of 1.4 to 2.1 kg per cm² and adults by snow with a crust strength of 2.1 to 2.8 kg per cm². Wolves walked on snow crusts with a strength of 1.1 kg per cm² and a 352-kg man wearing mocassins could walk on snow with a strength of 1.8 kg per cm².

2.2. Soil analysis

Soils at study plots and exclosures were extremely acid and all but one of the plots was on coarse sand. Except at Study Plot No. 10, magnesium and calcium were scarce. The caribou habit of gnawing cast antlers suggests that the calcium shortage may be important.

1. Snow

Essential to the assessment of the taiga winter range is an understanding of caribou food habits, movements, and behaviour as related to the winter environment. That environment is constantly changing as a result of seasonal variation in depth and density of snow and hardness of crust (Formosov, 1946; Pruitt, 1959). The character of the snow cover determines both the mobility of caribou and forage availability. Because caribou locate forage beneath the snow by smell (Skoog, 1968), snow condition plays an important role in the location of feeding craters as well as in the number of craters that can be dug at any one site (Pruitt, 1959).

In early winter caribou movements are not hindered by snow. Caribou move freely over their range. Crater enclosures showed that they did minimum damage to the terrestrial forage supply during that period. The preferred feeding sites appeared to be along stream and lake shores in dense stands of *Equisetum fluviatile* and *Carex aquatilis*.

As the snow depth increases caribou become confined to areas with the most favourable conditions (Henshaw, 1964). The critical limit of snow depth for caribou or reindeer is about 50 to 60 cm (Formosov, 1946; Pruitt, 1959; Henshaw, 1964). I observed that in about 50 cm of soft snow caribou were confined to established trails; that depth was attained between mid December and mid February and marked the change between the early and mid winter periods.

Caribou continue migrating during the early stages of mid winter; later their movements become less predictable. In 1967 Kaminuriak caribou continued migrating until mid April, whereas in 1968 they were relatively sedentary between February and May. Forage use differed between the two winters although snow depths were similar. In 1967 migrating caribou utilized forage along streams, lakes, muskegs, and meadows. Accessible feeding areas along well-used migration routes re-

ceived intense use but for only a short time. Longer and more intensive use of small feeding areas was made in 1968 when the herds were more sedentary. Rumen analyses showed that mosses were consumed in larger amounts and in greater variety during mid winter 1967 when the herds were migrating than in 1968 when they were more sedentary. This suggests use of different habitats. Aerial and ground observations of caribou feeding craters during the two winters confirmed this. Utilization of different habitats during separate winters is an important factor in determining range capacities.

In late winter when snow crusts had formed caribou adapted by foraging on arboreal lichens, and on white birch and willow along lake and stream shores. Caribou used those sources of forage infrequently until late winter and then intensively until spring. The extent of use of the above-snow forage depends on the density of caribou and the duration of the late-winter period. A delay in the softening of snow crusts could extend that period by as long as 3 weeks. Caribou became relatively sedentary each winter when the snow became generally crusted from thawing and freezing.

Caribou return to a terrestrial forage diet during early spring when the snow crust is softened by sun. The crust softens first on open southern exposures, especially at the bottom of old craters and on steep banks of eskers, lakes, and streams. Snow depths diminish rapidly at exposed sites and caribou seek out bare patches in old craters. Caribou re-use craters as long as the forage remains exposed and boundaries of craters show up clearly during the following summer. Steep south-facing exposed banks also become snow-free and caribou may use 50 per cent or more of the terrestrial lichen in those small, local areas. They graze bare banks even more repeatedly than old craters, and consume all but the smallest lichen podetia. They also intensively utilize vascular plants, especially *Vaccinium vitis-idaea*, on the exposed sites.

A third site that becomes exposed in early spring is the area at the base of a conifer, called "quamanig" by Pruitt (1959), where caribou graze on exposed lichens and vascular plants. In addition, according to summer observations, caribou dig in soft snow at the outer margins of spruce trees on the margins of "quamanig" and use the tall lichens that often grow there. Those lichens are more disarranged than heavily eaten, but crater margins are distinct. Caribou begin their migration towards the calving grounds about the same time that bare patches appear on the south-facing banks, and therefore damage is confined to a relatively small area along migration routes. Andreev (1961) stated that migrating reindeer keep strictly to areas where there are thawed patches and food is more easily obtainable and gradually move northward as the snow thaws.

2. Food habits

Studies of craters, cratered sites, and analyses of rumen contents collected during spring and early, mid and late winter have demonstrated that terrestrial lichens are the primary forage of caribou on the taiga winter range. However, caribou can thrive without lichens (Palmer, 1926; Murie, 1935; Skoog, 1968) and normally supplement their lichen diet with other plant foods. Use of non-lichen forage probably increases digestibility of lichens (Scotter, 1964). According to Druri (1960) and Ahti and Hepburn (1967) lichens alone are nutritionally inadequate to sustain caribou and reindeer for long, but Palmer (1926) and Poijarvi (1945) report that under protected conditions reindeer have thrived on lichens alone. If for no other reason than abundance and availability, terrestrial lichens are the most important winter food of the Kaminuriak Population.

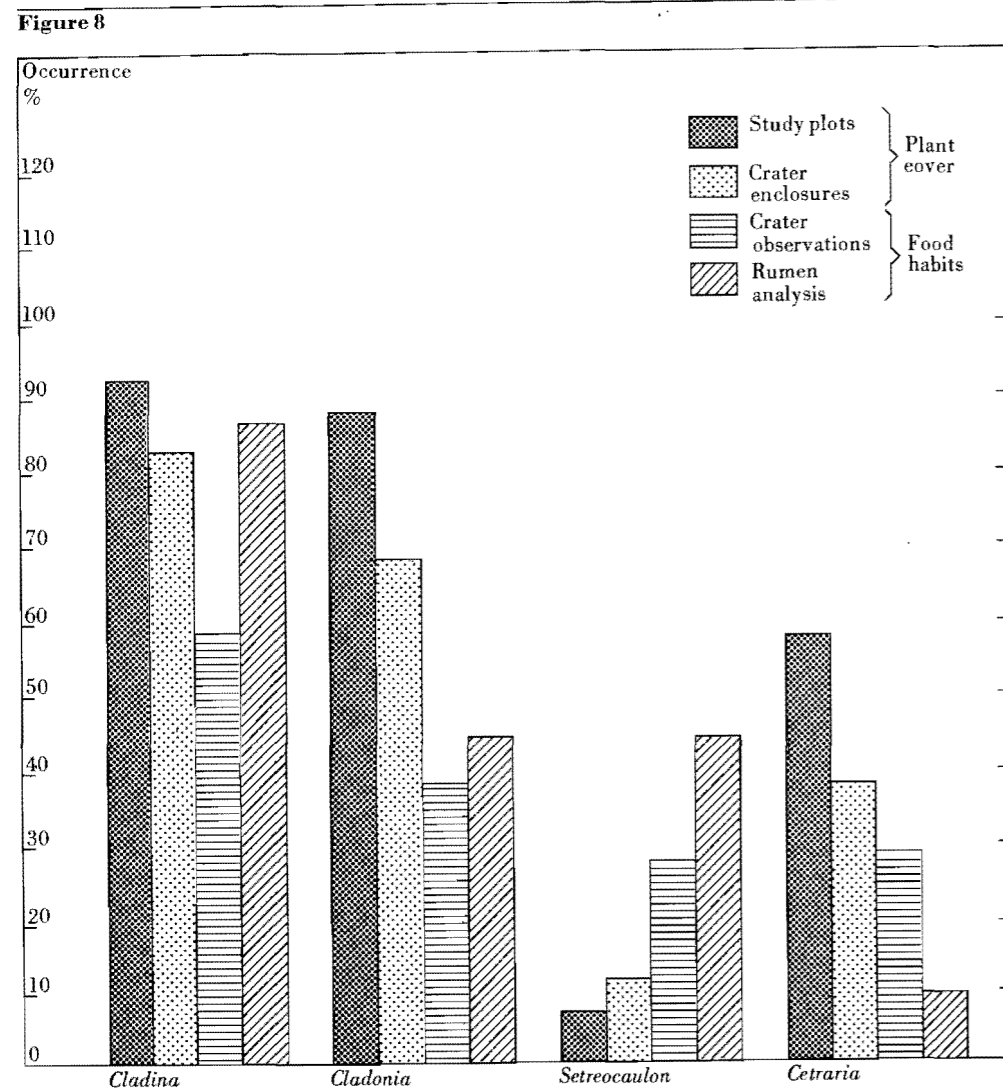
As was found by Scotter (1967), *Cladina* lichens made up the bulk of the winter rumen contents. They were also the dominant lichen group found on the taiga winter range. *Cladina mitis* and *Cladina alpestris* were the most abundant species

found on the study plots. Ahti (1959) found *Cladina mitis* in Newfoundland to be "a most abundant species owing to its rapid regeneration" and he believed it "to be the most important food-lichen of the caribou." *Cladina alpestris*, on the other hand, is a less preferred reindeer forage in Scandinavia and northwestern Manitoba (Scotter, 1965c), although in certain areas of Russia according to Kareev (1968) it is "reindeer's main lichen fodder during winter."

As a preferred caribou forage *Stereocaulon* is next to the *Cladina* spp. on the basis of its abundance in winter rumen samples and uneven distributions on the taiga (Fig. 8). Although there is a possible bias in the rumen analyses, as *Stereocaulon* is easily recognizable, crater observations in April at Hara Lake, Saskatchewan attest to its importance as late-winter forage. On favourable sites *Stereocaulon* recovers rapidly from caribou utilization or mechanical disturbance. It has a higher protein content than *Cladina* or *Cladonia*. Kareev (1968) states that *Stereocaulon paschale* in Russia "is considered as a good fodder for young animals and, in certain cases, included among the fattening varieties of fodder plants."

The manner in which caribou use terrestrial lichens is important. Some investigators (Andreev, 1954; Skuncke, 1963; Scotter, 1964; Skoog, 1968; Pegau, 1968a) suggest that they nip off the living portions of terrestrial lichens and lichen recovery from such grazing depends on the per cent of tips removed. I observed top-cropping of lichens only during a limited period in spring. During early and mid-winter periods the caribou plucks and eats the entire lichen podetium, with exception of the dead jelly-like portion. I observed this method of feeding in craters and confirmed it by rumen analyses. The dead portion of the lichen podetium and particularly the black portion of *Cladonia rangiferina* was common in rumen contents. Even the primary thallus, which is the portion of the lichen that is attached to the substrate, was common in winter rumen samples.

Figure 8
A comparison of percentage occurrence of the four most common lichen genera



Inclusion of the dead portions of lichen podetia as well as the living portions increases the potential lichen forage supply by 100 per cent (Scotter, 1963). During certain periods of early spring, however, caribou crop upper portions of exposed lichens from previously dug craters. Water appears in the thawed crater by day and freezes at night, and the exposed lichens thaw gradually from the top the following day. I observed top-cropping of lichens in

this study only during those limited periods of early spring, freeze-thaw conditions.

Arboreal lichens are an important source of winter forage in the taiga, especially in periods of extremely hard snow conditions during late winter (Hustich, 1951; Banfield, 1954; Cringan, 1957; Edwards and Ritcey, 1960). Arboreal lichens probably help to maintain a balanced rumen environment for micro-organisms during the period when terrestrial lichens are inac-

cessible. Scotter (1965b) found arboreal lichens to be relatively abundant in northwestern Manitoba, and I observed them to be more abundant there than in taiga caribou ranges of central Alaska.

Grass-like plants are the major non-lichen forage utilized in the taiga during early winter and occasionally during early spring. *Carex aquatilis* and *Equisetum fluviatile* are the primary grasslike plants used in northwestern Manitoba. *Carex aquatilis* is the most abundant sedge in the "marshlands" of the area (Baldwin, 1953). That plant provides the richest reserves of "undersnow" green vegetation for reindeer in parts of Russia (Kareev, 1968), and is also considered especially important to caribou in Alaska (Skoog, 1968). Loughrey (1952) reported *Equisetum* heavily used by wintering caribou at a site in northern Manitoba, and Skoog (1956) reported it heavily used in Alaska at all times of the year. In parts of Russia *Equisetum* is a good winter forage (Aleksandrova and Andreev, 1964) where it is eaten green as well as brown (Kareev, 1968). Aleksandrova and Andreev (1964) stated that "The ash is very rich in calcium, potassium, phosphorous and other elements of mineral nutrition." Baldwin (1953) listed *Equisetum fluviatile* as "common and abundant on alluvium of the Cochrane River and silted bays of the larger lakes" in northwestern Manitoba.

In mid winter, and more often in late winter and early spring, the major non-lichen forage items include leaves and twigs of woody plants. Leaves of *Vaccinium vitis-idaea* are the most utilized although moderate amounts of *Vaccinium myrtilloides*, and *V. uliginosum* are also consumed. Scotter (1965c) observed that caribou had stripped leaves from *Vaccinium vitis-idaea* in northern Saskatchewan, and he thought that it might be an important source of protein. Skuncke (1963) attaches high significance to that species as a winter forage for reindeer in Sweden. Baldwin (1953) found *Vaccinium vitis-idaea* one of the most common plants in the area he examined in northwestern Manitoba. Argus (1966) re-

ported it abundant in the area he studied in northeastern Saskatchewan. I found it to be the most common vascular plant in the study area.

I found *Ledum groenlandicum* to be common except on well-drained, sandy soils supporting jack pine, and Scotter (1964) also recorded it as a common plant on the taiga. Kelsall (1960) described it as a preferred forage of barren-ground caribou, and Simkin (1965) reported it as heavily used by woodland caribou in Ontario. Scotter (1964), although he found it in rumen samples, suggested that it may be eaten accidentally. Similarly my rumen analyses do not suggest that *Ledum groenlandicum* is important in the winter diet. Caribou often crater in sites dominated by *Ledum groenlandicum*, but I believe that the reason may be that they can detect other forage beneath deep snow more easily in the presence of *Ledum* shrubs, and craters are more easily excavated there than in sites free of intermediate-sized shrubs.

Woody twigs make up a large portion of non-lichen material found in rumens although differential digestion rates exaggerate their abundance (Bergerud and Russell, 1964). Caribou browse white birch and willow occasionally throughout the winter but especially during late winter when a hard snow crust covers much of the range. Twigs of *Salix* and *Betula* are listed as winter forage for caribou (Skoog, 1968) and reindeer (Herre, 1956; Andreev, 1954). Simkin (1965) stated that woodland caribou in Ontario utilize twigs of *Salix* spp. and *Alnus crispa*. White birch, dwarf birch, willow, and alder are fairly abundant along drainages, lake shores, and in recent burns throughout the taiga.

In years when mushrooms are abundant they may be important in the caribou winter diet. Entire, small mushrooms have been found in April caribou rumens and up to 10 per cent of the contents of November rumens have been comprised of mushrooms. Kareev (1968) stated that reindeer in Russia "unerringly detect and dig out the snow-covered shrunk and frozen

mushrooms." He listed mushrooms as a valuable, nutritive and vitamin-rich fodder. Although mushrooms are not consumed by caribou in large quantities during the winter they may, because of their high nutritional value (Larin, 1951), be a valuable supplement to a predominantly lichen, protein-scarce diet.

3. Lichen growth

Because lichens, principally *Cladina* and *Cladonia* spp., are the dominant forage of caribou in the taiga it is important to understand how the lichen podetium grows. Andreev (1954) explains how the *Cladina* podetium passes through three growth stages. The first stage is called the *growth-accumulation period* which lasts an average of 10 years and varies from 5 to 25 years. There is no dying off of the podetium during that period. The second stage is the *growth-renewal period* when the podetium grows at its highest rate. However, the podetium dies off at the base at a rate equal to the growth. That period lasts a long time, extending to 100 years or more. The third stage which may also exceed 100 years, is the *podetium degeneration period* when the podetium dies off at a greater rate than it grows. Andreev (1954), Ahti (1959), Scotter (1963), and Pegau (1968b) have measured growth rates of various *Cladina* spp. by the formula:

$$\frac{\text{Length of living podetium}}{\text{Number of nodes on living podetium}} = \text{Average annual linear growth rate of the podetium}$$

The average annual linear growth rate (mm) measured by Scotter (1965b) at four locations in northwestern Manitoba, ranged from 3.5 to 4.3 (*C. alpestris*) and 4.1 to 5.1 (*C. rangiferina*), which was slightly less than Pegau (1968b) found on the Seward Peninsula in (*C. rangiferina*). Scotter (1964), Pegau (1968b), and the present study have found considerable variation between growth rates of podetia on a single site. Factors that probably contribute to

variation in lichen growth include: the age of the podetium; the capacity of the podetium to compete with adjacent podetia; prior disturbance by animals including man; and site conditions such as substrate, drainage, and exposure. Another factor to be considered when annual linear growth is used in production calculations is the number of lateral branches. *C. alpestris* has many lateral branches compared with *C. rangiferina* or *C. mitis*, and could produce more forage annually even though the annual linear growth rate may be less.

4. Forest fires

The taiga winter range has a long history of forest fires (Scotter 1964, 1971), and Lutz (1956) mentions that their "repeated occurrence in prehistoric, historic and modern time is well substantiated." Pruitt (1959), Scotter (1964, 1971), Thomas (1967), and Kelsall (1968) have all remarked on the vast areas that have been burned in caribou winter ranges of the Canadian taiga and stated their concern about the detrimental effects on caribou populations.

It is difficult to locate an area of homogeneous cover of more than 4 hectares (10 acres) in the taiga winter range, partly because of the incidence of forest fires and partly due to variable drainage. Lutz (1956) wrote that "these differences in species, together with the heterogeneity of the pattern of burning—often more intense burning under spruce trees than in the intervening space between spruce trees—result in a mosaic of vegetation." I found the heterogeneity in northwestern Manitoba and northeastern Saskatchewan, and Watson (1962) found it in northcentral Saskatchewan. Heterogeneity of cover is important to wintering caribou. It ensures that forage will be available under conditions of snow depth and crust, which vary during (Fig. 7) and between winters. Areas that include a mosaic of cover types including loafing and escape areas, such as lakes and streams adjacent to feeding areas, are most important to caribou during mid and late winter and

are likely to attract caribou concentrations for extended periods of time.

The estimated percentage of land area burned annually on a study area in northern Manitoba during the 12-year period 1955–67 as measured from aerial photographs was 0.17 per cent, somewhat less than Beckel's (1958) estimate of 0.25 per cent for approximately the same area during the 20-year period 1935–66 (Table 16). In contrast, forest fires burned an estimated 0.87 per cent of land area annually from 1940 to 1955 on a study area in north-central Saskatchewan (Scotter, 1964). There is a great deal more upland in the Saskatchewan taiga winter range than that of Manitoba, and upland ranges are more susceptible than lowlands to lightning strikes. Some upland sites in both areas are more susceptible to lightning-caused fires than others and burn more frequently.

Both *Cladina alpestris* and *C. rangiferina* are climax lichen species that appear in stands 40 years or more after a fire, but there are a number of important lichens like *C. mitis* that become established earlier. Figure 4 shows that stands less than 40 years contained a standing crop of terricolous lichens equal to some stands twice that age, and stands less than 60 years old contained as large a crop as some stands over 120 years old. Standing crop of lichens may be related more to the degree of caribou utilization and the severity of the fire than to the number of years since the previous fire. This appears to be the case in enclosures 4, 5, and 6 which are in areas that had apparently burned at about the same time but supported different standing crops of lichens in 1967. The differences in standing crop are not reflected in differences in per cent lichen ground cover.

Forest fires can improve conditions for the growth of terrestrial lichens. Scotter (1965b) mentioned that fires tend to slow the transition from forest to muskeg thus favouring lichen production and that, "Some burned-over muskegs produce more lichens than were formerly present." Skuncke (1963) stated, in connection with

Table 16
Comparison of aerial photograph interpretations of samples of caribou winter range in taiga of northern Saskatchewan and northwestern Manitoba

Source	Northern Saskatchewan	Northwestern Manitoba	
	Scotter (1964) plus data in CWS files	Beckel (1958)	Present work
Film	Black and white	Black and white	Colour
Photograph Scale	1:50,000	1:60,000	1:15,840
Year photographed	1955	1955	1967
Total area (sq km)	12,727	11,432	12,106
Land area (sq km)	9,673	9,260	9,827
Water area %	24	19	19
Upland area (sq km)	8,169	5,185	5,406
Area burned (sq km)	1,261 (15 yr)	464 (20 yr)	192 (12 yr)
Area burned (%)	13	5	2
Area burned annually (%)	0.87	0.25	0.17

the third stage of lichen growth when the lichen mat is replaced by mosses, that forest fires "can eventually lead to regeneration, that is, to the growth of new lichen plants." Rowe and Scotter (1973) also mentioned that in the southern limit of winter range of barren-ground caribou, fires sometimes make land more productive of terrestrial lichens and other forage plants by removing carpets of bryophytes.

The accumulation of needles underneath old conifer trees favours the growth of vascular plants such as *Vaccinium vitis-idaea*, *Empetrum nigrum*, and *Arctostaphylos uva-ursi* as well as mosses. Fires could alter that condition in favour of lichen growth.

Concerning the effects of forest fires on soil, Lutz (1956) believed that it would be "impossible to prove" that soil destruction or deterioration occurred on the majority of burns in Alaska. He mentioned that there is usually a "reduction of soil acidity" after burns, a large increase of "exchangeable calcium in the upper layers of mineral soil," an increase in the "availability of nitrogen to vegetation" and that, "fires quickly make available the nutrient materials bound in organic matter." Even during the early years after a forest fire, early invaders such as fireweed (*Epilobium* spp.), *Vaccinium* spp., grass (*Calamagrostis canadensis*), and sucker growths of white birch are potential forage for caribou.

5. Condition of range

Caribou affected their taiga winter range little during this study. Rumen analyses and field observations have shown that caribou utilize forage according to its availability, which depends throughout winter on snow depth and condition. That relationship ensures against over utilization of any forage species over a wide area. In addition, such forages as grasslike plants and mushrooms are annual crops which appear unaffected by caribou utilization. Vascular plants such as *Vaccinium vitis-idaea*, *Salix* spp., and *Betula* spp. recover rapidly, and I saw no signs of permanent damage from browsing. Lichens, because they grow more slowly than vascular plants, would be expected to show the effects of caribou use more than other plants. However I observed no damage to lichen stands used by caribou in the presence of a complete snow cover. According to standing crop calculations of terrestrial lichens and the percentage coverage of lichens in the ground cover, a large reserve of potential lichen forage exists in the taiga. There is also a large reserve of potential arboreal lichen forage, Scotter (1965c).

Caribou can damage lichen stands locally during the spring migration when lichens become exposed on southern exposures of eskers, and stream and lake banks. Repeated use of lichens on such

sites has resulted in the establishment of dense stands of *Arctostaphylos uva-ursi* and *Empetrum nigrum*. Lichens are sparse and small if present at all. The phenomenon can be observed on eskers and steep lake and stream banks in much of northern Manitoba, especially in the forest-tundra.

Stereocaulon is an important lichen component in the caribou winter diet, although it is unevenly distributed and relatively scarce compared with *Cladonia*, *Cladina*, or *Cetraria* (Fig. 8). *Stereocaulon* recovers from grazing more readily than *Cladonia*, *Cladina*, or *Cetraria*. Ritchie (1959) suggested that *Stereocaulon* might be an indicator of over-use by caribou. Scotter (1965b) agreed in part with Ritchie that the abundance of *Stereocaulon* on some sites may be the result of intensive grazing by caribou. Scotter suggested, however, that in some sites moisture was the cause of *Stereocaulon* dominance. My observations support the idea of a relationship between caribou grazing and *Stereocaulon* abundance especially in respect to intensive use of exposed lichen stands in early spring. Small, pure, or nearly pure stands of *Stereocaulon* are occasionally encountered on sparsely treed sites on southern slopes of inhabited caribou range, but I have not observed them on similar sites immediately to the south of caribou range. I believe that, conversely, the presence of pure stands of climax lichens, *Cladina alpestris* and *C. rangiferina*, indicates that there has not been more than light recent use by caribou.

I have observed no taller or more continuous cover of terrestrial lichens on caribou and reindeer ranges in Alaska and Quebec than in northwestern Manitoba and northeastern Saskatchewan. One explanation for the favourable conditions of lichen stands on the Manitoba and Saskatchewan ranges is that they are used only in winter when snow cover minimizes the effects of grazing and trampling. Pruitt (1959) has commented on the protective influence of snow cover and cold temperatures on forage stands used by caribou,

Lush terrestrial lichen growth between mature spruce. Note the reduction of vascular plants between trees and the increase beneath trees



and Pegau (1970) has shown the detrimental influence of grazing and trampling by reindeer during the summer on Alaska lichen ranges. Deep trails free of vegetation on ridges and southern slopes in northern Manitoba and Saskatchewan attest to the effects of trampling on snowfree sites. Another factor, perhaps more important, favouring lichens in northern Manitoba and Saskatchewan is that the growing conditions favour them over vascular plants. Lichens can tolerate periods of dessication on the predominantly sandy soils better than vascular plants and mosses (Ahti and Hepburn, 1967).

6. Capacity of the taiga range

It is difficult to estimate carrying capacity of the taiga range because caribou use it differently each winter. The number of caribou that enter the taiga varies from year to year as does the time the caribou spend there. Their distribution, density, and food habits vary according to snow conditions. However, by calculations based on reindeer ranges with known stocking

rates over extended periods of time, Poirjarvi (1954) and Andreev (1954) in Russia and Skuncke (1963) in Sweden, estimated that 8 hectares (20 acres) of lichen range were required to sustain each reindeer during winter. Helle (1966), who considered the effects of snow on availability and utilization of forage, estimated that 10 to 15 hectares (25 to 37 acres) of lichen winter range were needed to support each reindeer in Finland. "Reindeer" lichens grow on the average of 3 to 5 mm annually in forest zones of Finland, which is similar to northwestern Manitoba (Scotter 1965c). Therefore by extrapolation from Helle's figures (10–15 hectares/reindeer/winter) the 12,113 km²-area in northwestern Manitoba assessed from coloured aerial photographs could support 36,000 to 53,000 caribou on the 5,407 km² of upland regions that had not burned in the past 20 years. By extrapolating the proportion of upland lichen range not burned in the past 20 years to the entire 121,704 km² taiga range (Parker, 1972) we can estimate carrying capacity at 360,000 caribou. That estimate,

which precludes caribou use of non-lichen forage as well as lichen forage on all lowlands and on uplands which had burned less than 20 years ago, is over 500 per cent greater than the 1968 estimate of the Kaminuriak Population (Parker, 1972).

Parker (1972) showed that during 4 months in the winter of 1967-68 some 50,000 caribou remained within an area of 9,303 km² for a density of 177 caribou per km². My visual observations within that area during February and again in April to May 1968, along with summer observations of crater enclosures, showed that less than 25 per cent of the terrestrial lichen range had been grazed or trampled. A year later only the most heavily grazed spring craters and southern exposed banks comprising about 10 per cent of the lichen range used, showed little or no vegetative recovery while the remaining 90 per cent showed rapid regeneration. Southern exposed banks, which had sustained intensive use by caribou during spring 1968, supported an active growth of primary lichen thalli in July 1969. In addition, many of the fragmented podetia in the spring craters used repeatedly by caribou had become anchored to the substrate and showed growth by July 1969.

Skoog (1968) observed that caribou used only two per cent of a feeding area during February to March in a heavily used part of Alaska. He stated of Alaskan caribou that, "there is little evidence to suggest that grazing itself has caused much damage," and goes on to say that "Most range damage can be assigned to the effects of trampling and trailing." The above is consistent with the restriction of damage found in the present study to lichen stands that first become bare in spring. Caribou sometimes suffer from unavailability of food under certain snow conditions. But it seems doubtful that under present conditions of caribou numbers and vegetation that such unavailability is related to the total forage reserves or the effects of fires on them. Snow characteristics on the taiga as well as influencing

availability of forage also affect the vulnerability of caribou to predators, including man. The fact that in some years the majority of caribou in the Kaminuriak Population have wintered on the tundra also suggests that dependency on taiga forage supplies is minor at present population levels.

Summary

The taiga winter range of the Kaminuriak Population is in northern Manitoba, northeast Saskatchewan, southeast Mackenzie District and southwest Keewatin District. I studied portions of northwestern Manitoba and northeastern Saskatchewan during this investigation.

The winter range in northwestern Manitoba is roughly 20 per cent water, 40 per cent lowland and 40 per cent upland. Lowland areas include 80 per cent muskeg and 20 per cent meadow whereas the upland is 80 per cent spruce and 20 per cent jack pine. The upland areas are primarily semi-open to open lichen woodland. Between 1955 and 1967, according to aerial photograph interpretations of the same 9,200-km² land area, 192 km² or 2.1 per cent of the area burned in 47 different forest fires.

Terrestrial lichens covered 50 to 90 per cent of the ground at 6 caribou enclosures and 23 of 25 study plots located in spruce, spruce and jack pine, and jack pine cover types. *Cladina* lichens, primarily *C. mitis* and *C. alpestris*, were the most abundant in the plots and enclosures. *Cladonia* spp. mainly *C. gracilis*, were common but only occasionally abundant. *Cetraria* lichens were common but not abundant, whereas *Stereocaulon* and *Peltigera* lichens were neither common nor abundant.

The standing crop of terrestrial lichens at the study plots and enclosures ranged from 2,000 to 7,000 kg dry weight per ha at all but two plots. The protein content in lichen samples ranged from 3.20 per cent in *Cladonia* spp. to 16.26 per cent in primarily *Stereocaulon paschale* samples. *Stereocaulon* samples also contained a higher amount of energy than *Cladonia*, *Cladina*, or *Cetraria* samples.

Lichen regeneration of primary thalli on artificially denuded 1-m² plots occurred on all plots after three growing seasons and covered from 10 to 75 per cent of the plot. Secondary thalli or podetia appeared on 66 per cent of the plots after three growing seasons. Primary thalli and in one instance a podetium were observed on caribou pel-

lets after three summer growing seasons. Removal of the stems and leaves of *Ledum groenlandicum* stimulated lichen growth whereas removal of only the leaves did not show a change in lichen growth.

Caribou rumen analyses showed that terrestrial lichens, primarily *Cladina* spp. and to a lesser extent *Cladonia* spp. made up the bulk of the winter diet on the taiga. *Stereocaulon* was also an important food, especially during April according to a comparison of its abundance in rumens and its occurrence in the taiga. Twigs and leaves of woody plants as well as grasslike plants were also important winter forages, and mushrooms were eaten when encountered. Seasonal availability appeared to dictate forage use by caribou after early winter.

The availability of forage depends on the depth, density, and crust hardness of snow as well as the proximity of travel routes, and treeless loafing and escape areas. Forage availability does not limit use in early winter, but as soon as snow depths reach about 50 cm various sites become unavailable. *Equisetum fluviatile* and *Carex aquatilis*, preferred forage during the early winter, become less available in mid winter along the drifted shores of lakes and streams. Caribou remain close to loafing and escape areas and therefore make little use of large areas of continuous tree cover. In late winter with the lengthening of day-light hours a crust forms on the snow and caribou change to a diet of arboreal lichens and woody browse. As soon as the crust softens caribou return to a diet of terrestrial forage using south exposures of stream-, lake-, and esker banks as well as old craters on exposed upland sites. In addition, the boles of conifer trees become exposed and are heavily used. Crater enclosures constructed during the early, mid and late winter and spring periods showed that the late winter and spring periods were the only time that the caribou damaged their forage stands. In late winter, arboreal lichen and woody browse crops were depleted locally and in spring the terrestrial forage crop was depleted on exposed sites along the migration routes.

The heterogeneity of plant cover in the taiga of northwestern Manitoba and northeastern Saskatchewan makes it well suited to sustain caribou use during the winter season because it offers caribou a wide range of depth, density, and hardness of snow. Forest fires help to maintain the heterogeneity.

Literature cited

Ahti, T. 1959. Studies on the caribou lichen stands of Newfoundland. Ann. Bot. Soc. Vanaina, 30:1-44.

Ahti, T., and R. L. Hepburn. 1967. Preliminary studies of woodland caribou range, especially on lichen stands in Ontario. Ont. Dep. Lands For. Res. Rep. (Wildl.) No. 74. 135 p.

Aleksandrova, V. D., and V. N. Andreev. 1964. Forage characteristics of the plants in the far north of the U.S.S.R. [Transl. Russ.] Izdatel'stvo Nanka. Can. Wildl. Serv.

Andreev, V. N. 1954. The growth of forage lichens and the methods for their regulation. Tr. Bot. Inst. An. SSSR, Acta Inst. Botan. Acad. Sci., USSR, Ser. 111. Geobotanika 9:11-74.

Andreev, V. N. 1961. The study of reindeer populations and migration routes by aerial methods. Zoologicheskii Zhurnal 40:117-121.

Argus, G. W. 1966. Botanical investigations in northeastern Saskatchewan: The subarctic Patterson-Hasbala lakes region. Can. Field-Nat. 80:119-143.

Baldwin, W. K. W. 1953. Botanical investigations in the Reindeer-Nueltin lakes area, Manitoba. Nat. Mus. Can. Bull. 128:110-142.

Banfield, A. W. F. 1954. Preliminary investigation of the barren-ground caribou. Can. Wildl. Ser. Wildl. Manage. Bull. Ser. 1, No. 10A and 10B.

Beckel, D. K. B. 1958. A pilot study of caribou winter range, Brochet, Manitoba. Can. Wildl. Serv. unpubl. rep. C-919. 41 p.

Bergerud, A. T., and L. Russell. 1964. Evaluation of rumen food analysis for Newfoundland caribou. J. Wildl. Manage. 24:809-814.

Brown, R. J. E. 1960. The distribution of permafrost and its relation to air temperature in Canada and the U.S.S.R. Arctic 13:163-177.

Cringan, A. T. 1957. History, food habits and range requirements of the woodland caribou of continental North America. N. Amer. Wildl. Conf. 22:485-501.

Daubenmire, C. 1959. A canopy-coverage method of vegetation analysis. Northwest Sci. 33:43-64.

Druri, L. M. 1960. Changes with age and season in the live weight of reindeer. A. N. Severtsov Inst. Animal Morphology. No. 31.

Edwards, R. Y., and R. W. Ritecy. 1960. Foods of caribou in Wells Gray Park, British Columbia. Can. Field-Nat. 74(1):3-7.

Engen, E. 1964. A brief report on the construction of three barren-ground caribou range enclosures in the Horseshoe Lake area of northern Manitoba. Man. Game. Br. 6 p.

Engen, E. 1965. A report on the construction of three barren-ground caribou range enclosures in the Lac Brochet area of northern Manitoba. Game Br. 6 p.

Formozov, A. N. 1946. Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds. Materials for fauna and flora of the U.S.S.R. Moscow Society of Naturalists, New Series, Zoology 5:1-152.

Helle, R. 1966. An investigation of reindeer husbandry in Finland. Acta Lapponica Fenniae No. 5. 65 p.

Henshaw, J. A. 1964. An environmental study of wintering caribou in northwestern Alaska. Unpubl. M.S. thesis. Institute of Biology, London, England. 154 p.

Herre, W. 1956. Rentiere. Die neue Brehm-Bucherei. A Ziemsen Verlag, Wittenberg. 47 p.

Hustich, J. 1951. The lichen woodlands in Labrador and their importance as winter pastures for domesticated reindeer. Acta Geogr. 12:1-48.

Karcev, G. T. 1968. Reindeer fodder resources. Pages 129-176 in P.S. Zhigunov, editor. Reindeer Husbandry.

Kelsall, J. P. 1960. Co-operative studies of barren-ground caribou 1957-58. Can. Wildl. Serv. Wildl. Manage. Bull. Ser. 1, No. 15. 145 p.

Kelsall, J. P. 1968. The migratory barren-ground caribou of Canada. Dep. Indian Affairs Northern Devel. Can. Wildl. Serv. Monogr. No. 3. 340 p.

Larin, I. V. 1951. Forage Plants of the meadow and pasture lands of the U.S.S.R. All-Union Research Institute of Forage Plants. State Agri. Publ. House. Moscow. Vol. 2. 648 p.

Loughrey, A. G. 1952. Caribou winter range study, 1951-1952. Can. Wildl. Serv. unpubl. rep. 30 p.

Lutz, H. J. 1956. Ecological effects of forest fires in the interior of Alaska. US Dep. Agr. Tech. Bull. No. 1133. 121 p.

Miller, D. R., and J. R. Robertson. 1967. Results of tagging caribou at Little Duck Lake, Manitoba. J. Wildl. Manage. 31:150-159.

Miller, F. L. 1974. Biology of the Kaminuriak population of barren-ground caribou. Part 2: Dentition as an indicator of age and sex; age composition and socialization of the population. Can. Wildl. Serv. Rep. Ser. 31. 88 p.

Murie, O. J. 1935. Alaska-Yukon caribou. N. Am. Fauna No. 54. US Govt Printing Office. Washington, D.C. 94 p.

Palmer, L. J. 1926. Progress of reindeer grazing investigations in Alaska. US Dep. Agr. Bull. 1423. 32 p.

Parker, G. R. 1972. Biology of the Kaminuriak population of barren-ground caribou. Part 1. Total numbers, mortality, recruitment, and seasonal distribution. Can. Wildl. Serv. Rep. Ser. 20. 95 p.

Pegau, R. E. 1968a. Reindeer range appraisal in Alaska. M.S. Thesis. Univ. Alaska. College, Alaska. 130 p.

Pegau, R. E. 1968b. Growth rates of important reindeer forage lichens on the Seward Peninsula, Alaska. Arctic 21:255-259.

Pegau, R. E. 1970. Effects of reindeer trampling on tundra vegetation. Ann. meeting Amer. Soc. Range Manage. p. 6. 23 (Abstract): 6.

Pojarvi, I. 1945. The consumption of lichens by reindeer kept on lichen feed from autumn to spring. State Agri. Experiment Activ. Bull. 205. Helsinki, Finland. 10 p.

Pruitt, Jr., W. O. 1959. Snow as a factor in the winter ecology of the barren-ground caribou (*Rangifer arcticus*). Arctic 12:158-179.

Ritchie, J. C. 1959. The vegetation of northern Manitoba 111. Studies in the Subarctic. Arct. Inst. N. Amer. Tech. Pap. No. 3. 55 p.

Ritchie, J. C. 1962. A geobotanical survey of northern Manitoba. Arct. Inst. N. Amer. Tech. Pap. No. 9. 48 p.

Rowe, J. S. 1959. Forest regions of Canada. Dep. Northern Affairs Nat. Resources. Ottawa. Forestry Br. Bull. 123:1-71.

Rowe, J. S., and G. W. Scotter. 1973. Fire in the boreal forest. Quaternary Res. 3:444-464.

Scotter, G. W. 1963. Growth rates of *Cladonia alpestris*, *C. mitis*, and *C. rangiferina* in the Taltson River region, N.W.T. Can. J. Bot. 41:1199-1202.

Scotter, G. W. 1964. Effects of forest fires on the winter range of barren-ground caribou in northern Saskatchewan. Can. Wildl. Serv., Wildl. Manage. Bull. Ser. 1, 18:1-111.

Scotter, G. W. 1965a. A plant collection from Cochrane River region of northwestern Manitoba. Blue Jay 23:96-100.

Scotter, G. W. 1965b. Study of the winter range of barren-ground caribou with special reference to the effects of forest fires. Can. Wildl. Serv. Unpubl. Rep. 81 p.

Scotter, G. W. 1965c. Reindeer ranching in Fennoscandia. J. Range Manage. 18:301-305.

Scotter, G. W. 1967. The winter diet of barren-ground caribou in northern Canada. Can. Field-Nat. 81:33-39.

Scotter, G. W. 1968. Effects of forest fires on the lichen winter ranges of barren-ground caribou in northern Canada. Ph.D. Thesis. Utah State Univ. 120 p.

Scotter, G. W. 1971. Fire, vegetation, soil and barren-ground caribou relations in northern Canada. Pages 209-230 in C. W. Slaughter, P. J. Barney and G. M. Hansen (eds.). Fire in the northern environment - a symposium. Pacific Northwest Forest Range Exp. Sta., Portland, Oregon.

Simkin, D. W. 1965. A preliminary report of the woodland caribou study in Ontario. Section Rep. (Wildl.) No. 59. 75 p.

Skoog, R. O. 1956. Range, movements, population and food habits of the Steese - Fortymile caribou herd. M.S. Thesis. Univ. Alaska, Fairbanks. xii and 145 p.

Skoog, R. O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. Ph.D. Thesis, Univ. California, Berkeley. 699 p.

Skuncke, R. 1963. Renbetet, marklavarna och skogsbracket Lappvasendent-Renforskningen no. 8:149-262.

Thomas, D. C. 1967. Population estimates of barren-ground caribou March to May, 1967. Can. Wildl. Serv. Rep. Ser. no. 9. 44 p.

Watson, G. H. 1962. An investigation of the possibilities of mapping caribou winter range from aerial photographs. Can. Wildl. Serv. Unpubl. Rep. 19 p.

Appendices

Appendix 1						
Forest type, location, topography, density, size, and age of trees in study plots and enclosures						
Plot	Location	Topography	No. trees per acre	Mean-ht., m.	Mean d.b.h., cm.	Age, yr.
Upland spruce						
1	Cochrane River	High esker	284	8.3	10.9	78
2	Lac Brochet	Flat	663	7.8	11.1	94
3	Lac Brochet	Flat	3,174	6.8	9.6	135
4	Lac Brochet	West slope, 5°	237	10.7	16.3	139
5	Lac Brochet	West slope, 8°	2,574	7.8	10.4	132
6	Lac Brochet	Flat	395	9.9	17.5	91
7	Lac Brochet	Flat	16	8.7	14.7	78
8	Fort Hall Lake	West slope, 3°	189	9.1	16.7	61
Lowland spruce						
9	Cochrane River	East slope, 5°	2,337	8.4	8.9	65
10	Cochrane River	West slope, 5°	932	4.9	7.8	76
11	Lac Brochet	West slope, 5°	1,279	9.6	14.2	181
12	Lac Brochet	West slope, 5°	1,105	10.1	14.5	129
13	Lac Brochet	West slope, 2°	742	9.8	12.7	79
14	Lac Brochet	Flat	379	8.9	13.7	78
Mixed spruce and jack pine						
15	Cochrane River	West slope, 12°	237	9.7	14.2	96
16	Cochrane River	Esker, NE slope, 3°	1,042	10.8	10.2	59
17	Lac Brochet	West slope, 2°	853	9.9	17.2	61
18	Lac Brochet	Hill top, flat	347	10.4	20.1	132
19	Horseshoe Lake*	South slope, 5°	221	10.2	17.0	58
Jack pine						
20	Cochrane River	Lowland flat	395	9.6	12.9	84
21	Cochrane River	Lowland flat	1,295	8.1	6.9	80
22	Cochrane River	Lowland flat	711	9.0	10.2	78
23	Lac Brochet	Hill, east slope, 5°	1,753	6.4	10.2	30
24	Horseshoe Lake	South slope, 2°	742	9.9	14.0	90
25	Horseshoe Lake	Hill, east slope, 2°	1,405	6.0	9.1	38
Jack pine						
Encl. 1	Horseshoe Lake	Gradual south slope, 2°	742	9.9	14.0	90
Encl. 2	Horseshoe Lake	Low hill, east slope, 2°	1,405	6.0	9.1	38
Mixed spruce and jack pine						
Encl. 3	Horseshoe Lake	Gradual south slope, 5°	221	10.2	17.0	58
Spruce, well drained						
Encl. 4	Lac Brochet	Low hill top, flat	3,174	6.8	9.6	135
Encl. 5	Lac Brochet	Gradual west slope, 5°	237	10.7	16.2	139
Encl. 6	Lac Brochet	Gradual west slope, 8°	2,574	7.8	10.4	132

* Also named Hjalmarson Lake.

Appendix 2												
Percentage cover of plant species occurring in more than four study plots or enclosures												
Plot no.	Lichens	Liver-worts	Mosses	Litter	<i>Vaccinium-vitis-idaea</i>	<i>V. myrtilloides</i>	<i>V. uliginosum</i>	<i>Ledum groenlandicum</i>	<i>Empetrum nigrum</i>	<i>Geocaulon lividum</i>	Mushrooms (no. per ha.)	
											1967	1969
1	24	2	5	10	12	5		Tr			15	
2	81	3	Tr	15	23	3	1		1		64	30
3	86	2	2	12	24	4	4	1			20	
4	81	3	Tr	19	30	20	Tr	7			20	25
5	84	5		14	33			14			20	54
6	75	3	3	17	28						30	86
7	80		5	16	29			54			15	
8	58	4	20	34	23		Tr	17				
9	70	Tr	22	7	23	4	16	35	1		138	
10	21		68	25	21		1	11	4	2	133	0
11	18		79	18	43			35			89	94
12	82	15	2	11	26		5	6			10	151
13	79	Tr	9	19	31		4	29			111	151
14	70		11	36	17			30			12	37
15	48	1	3	13	23		5			Tr	42	0
16	81	4	5	10	50	2		6		Tr	74	134
17	76		2	30	36	12	23	1	1		96	153
18	77		Tr	40	33	10	7	Tr		1	32	25
19	92		2	19	5	7					12	
20	62		7	32	16					2	25	0
21	72	1	2	39	39				3	2	108	99
22	79	Tr	5	22	30				4	1	131	0
23	64	Tr		69	37	12		3			72	47
24	88		Tr	29	2	10					37	235
25	80		3	45	1	9					20	
Encl. 1	85	5	Tr	34	4	1		3			82	
Encl. 2	80		5	38	5	20					30	
Encl. 3	79			24	18							
Encl. 4	86	3	1	9	26		10	1	Tr		37	
Encl. 5	70	5		32	35	9		6			20	40
Encl. 6	84		15	43		2	1	8			22	69

Appendix 3

Mean and range of percentages by weight of major lichen genera in study plots and enclosures

	<i>Cladina</i>	<i>Cladonia</i>	<i>Stereocaulon</i>	<i>Cetraria</i>	<i>Peltigera</i>
Plot 1	77	20	0	3	0
2	86	5	8	7	0
3	90	3	0	7	0
4	83	16	0	1	0
5	89	5	0	6	0
6	48	43	0	9	0
7	76	24	0	0	0
8*					
9	85	15	0	Tr	0
10	42	58	0	0	0
11	47	20	0	0	33
12	66	34	0	0	0
13	52	16	0	32	0
14	53	10	0	37	0
15	70	28	2	Tr	0
16	90	7	0	3	0
17	73	15	0	12	0
18	77	18	0	5	0
19	73	24	0	3	0
20	62	38	0	0	0
21	93	5	0	2	0
22	78	12	10	0	0
23	65	35	0	0	0
24	73	22	0	5	0
25	53	42	0	5	0
Encl. 1	70	28	0	2	0
2	78	20	0	2	0
3	79	16	0	5	0
4	60	21	0	19	0
5	90	10	0	Tr	0
6	87	8	0	5	0

* Divot samples were not collected from Plot 8.

Appendix 4

Location and forage plant cover of 1-m² plots established in 1967

Plot No.	Date established	Place	Lat.	Long.	Forage plants in sample
1	June 19	Lac Brochet	58°39'15"	101°37'15"	Lichen, 75% <i>Cladina alpestris</i>
2	June 19	Lac Brochet	58°39'15"	101°37'15"	Lichen, 95% <i>Stereocaulon paschale</i>
3	June 19	Lac Brochet	58°39'15"	101°37'15"	Lichen, 50% <i>Cladina rangiferina</i>
4	June 19	Lac Brochet	58°39'15"	101°37'15"	Lichen, 50% <i>Cetraria nivalis</i>
5	June 20	Lac Brochet	58°39'15"	101°37'15"	Lichen, mixed species
6	June 20	Lac Brochet	58°39'45"	101°35'20"	Lichen, mixed species
7	June 20	Lac Brochet	58°39'45"	101°35'20"	Lichen, 75% <i>Stereocaulon paschale</i>
8	June 21	Lac Brochet	58°39'45"	101°35'20"	Lichen mixed species
9	June 21	Lac Brochet	58°40'20"	101°34'40"	Lichen, mixed <i>Cladonia</i> , <i>Cladina</i> & <i>Cetraria</i>
10	June 21	Lac Brochet	58°39'15"	101°37'15"	<i>Ledum groenlandicum</i>
11A	June 22	Lac Brochet	58°39'15"	101°37'15"	<i>Vaccinium vitis-idaea</i>
11B	June 22	Lac Brochet	58°39'15"	101°37'15"	<i>Empetrum nigrum</i>
12	June 25	Lac Brochet	58°39'45"	101°35'20"	Lichen, mixed species
13	June 25	Lac Brochet	58°40'20"	101°34'40"	Lichen, mixed species
14	June 26	Lac Brochet	58°39'30"	101°35'40"	Lichen, mixed <i>Cladonia</i> , <i>Cladina</i>
16	June 28	Horseshoe Lake*	57°42'45"	101°12'30"	Lichen, mixed species
17	June 28	Horseshoe Lake	57°41'20"	101°12'30"	Lichen, mixed species
18	June 28	Horseshoe Lake	57°38'45"	101°11'15"	Lichen, mixed species
19	Sept. 17	Lac Brochet	58°40'30"	101°35'15"	<i>Carex aquatilis</i>
20	Sept. 17	Lac Brochet	58°39'45"	101°35'15"	<i>Carex aquatilis</i>
21	Sept. 18	Lac Brochet	58°40'10"	101°37'15"	<i>Carex aquatilis</i>
22	Sept. 18	Lac Brochet	58°40'	101°37'	<i>Equisetum fluviatile</i>
23	Sept. 18	Lac Brochet	58°39'15"	101°37'15"	<i>Ledum groenlandicum</i>
24	Sept. 23	Cochrane River	58°19'30"	101°12'15"	<i>Equisetum fluviatile</i>
25	Sept. 24	Cochrane River	58°19'15"	101°12'	<i>Equisetum fluviatile</i>

* Also named Hjalmarson Lake.

Other publications in the Report Series

- No. 1*
Whooping crane population dynamics on the nesting grounds, Wood Buffalo National Park, Northwest Territories, Canada by N. S. Novakowski
Cat. No. R65-8/1, Price 50¢
- No. 2*
Bionomics of the sandhill crane by W. J. D. Stephen
Cat. No. R65-8/2, Price 75¢
- No. 3*
The breeding biology of Ross' goose in the Perry River region, Northwest Territories by J. P. Ryder
Cat. No. R65-8/3, Price 75¢
- No. 4*
Behaviour and the regulation of numbers in blue grouse by J. F. Bendell and P. W. Elliott
Cat. No. R65-8/4, Price \$1.00
- No. 5*
Denning habits of the polar bear (*Ursus maritimus* Phipps) by C. R. Harington
Cat. No. R65-8/5, Price 50¢
- No. 6*
Saskatoon wetlands seminar
Cat. No. R65-8/6, Price \$5.25
- No. 7*
Histoire naturelle du Gode, *Alca torda*, L., dans le golfe Saint-Laurent, province de Québec, Canada par J. Bédard
Cat. No. R65-8/7, Price \$1.25
- No. 8*
The dynamics of Canadian arctic fox populations by A. H. Macpherson
Cat. No. R65-8/8, Price \$1.00
- No. 9*
Population estimates and distribution of barren-ground caribou in Mackenzie District, N.W.T., Saskatchewan, and Alberta — March to May, 1967 by D. C. Thomas
Cat. No. R65-8/9, Price \$1.00
- No. 10*
The mammals of Jasper National Park, Alberta by J. D. Soper
Cat. No. R65-8/10, Price \$2.50
- No. 11*
Causes and implications of an observed sex differential in the survival of wapiti by D. R. Flook
Cat. No. R65-8/11, Price \$1.25
- No. 12*
Breeding biology of California and ring-billed gulls: a study of ecological adaptations to the inland habitat by K. Vermeer
Cat. No. R65-8/12, Price \$1.25
- No. 13*
Geographical variation in the polar bear (*Ursus maritimus* Phipps) by T. H. Manning
Cat. No. R65-8/13, Price \$1.00
- No. 14*
Studies of bird hazards to aircraft
Cat. No. R65-8/14, Price \$1.25
- No. 15*
Moose and deer behaviour in snow in Fundy National Park, New Brunswick by J. P. Kelsall and W. Prescott
Cat. No. R65-8/15, Price \$1.00
- No. 16*
Effects of phosphamidon on forest birds in New Brunswick by C. D. Fowle
Cat. No. CW65-8/16, Price \$1.00
- No. 17*
Populations, movements and seasonal distribution of mergansers in northern Cape Breton Island by A. J. Erskine
Cat. No. CW65-8/17, Price \$1.00
- No. 18*
Waterfowl habitat trends in the aspen parkland of Manitoba by W. H. Kiel, Jr., A. S. Hawkins and N. G. Perret
Cat. No. CW65-8/19, Price \$1.25
- No. 19*
Vegetation of the Ngorongoro Conservation Area, Tanzania by D. J. Herlocker and H. J. Dirschl
Cat. No. CW65-8/19, Price \$1.25
- No. 20*
Biology of the Kaminuriak Population of barren-ground caribou.
Part 1: Total numbers, mortality, recruitment, and seasonal distribution by G. R. Parker
Cat. No. CW65-8/20, Price \$1.50
- No. 21*
Food habits and ecology of wolves on barren-ground caribou range in the Northwest Territories by E. Kuyt
Cat. No. CW65-8/21, Price \$1.00
- No. 22*
Background for managing grizzly bears in the national parks of Canada by K. R. D. Mundy and D. R. Flook
Cat. No. CW65-8/22, Price \$1.00
- No. 23*
The mammals of Waterton Lakes National Park, Alberta by J. D. Soper
Cat. No. CW65-8/23, Price \$1.25
- No. 24*
Feeding ecology of Pintail, Gadwall, American Widgeon and Lesser Scaup ducklings in southern Alberta by L. G. Sugden
Cat. No. CW65-8/24, Price \$1.50
- No. 25*
Home range and breeding biology of the Shoveler by H. J. Poston
Cat. No. CW65-8/25, Price \$1.50
- No. 26*
Calf mortality during 1970 on the calving ground of the Kaminuriak caribou by F. L. Miller and E. Broughton
Cat. No. CW65-8/26, Price \$1.00
- No. 27*
Bird damage to fruit crops in the Niagara Peninsula by R. G. B. Brown
Cat. No. CW65-8/27, Price \$1.50

- No. 28*
Migration of Lesser Snow and Blue Geese in spring across southern Manitoba
Part 1: Distribution, chronology, directions, numbers, heights and speeds by H. Blokpoel
Cat. No. CW65-8/28, Price \$1.00
- No. 29*
CWS Waterfowl studies in eastern Canada, 1969-73 edited by H. Boyd
Etude du SCF sur les oiseaux aquatiques dans l'est du Canada 1969-73 rédigé par H. Boyd
Cat. No. CW65-8/29, Price/Prix \$3.00
- No. 30*
Landscape classification and plant successional trends in the Peace-Athabasca Delta by H. J. Dirschl, D. J. Dabbs and G. C. Gentle
Cat. No. CW65-8/30, Price \$3.00
- No. 31*
Biology of the Kaminuriak Population of barren-ground caribou.
Part 2: Dentition as an indicator of age and sex; composition and socialization of the population by F. L. Miller
Cat. No. CW65-8/31, Price \$3.00
- No. 32*
Migration of Lesser Snow and Blue Geese in spring across southern Manitoba.
Part 2: Influence of the weather and prediction of major flights by H. Blokpoel and Maureen C. Gauthier
Cat. No. CW65-8/32, Price \$1.00
- No. 33*
An investigation of caribou range on Southampton Island, Northwest Territories by G. R. Parker
Cat. No. CW65-8/33, Price \$2.75
- No. 34*
The northern interior grizzly bear *Ursus arctos* L. by A. M. Pearson
Cat. No. CW65/8-34, Price \$4.50
- No. 35*
The nesting population of Lesser Snow Geese in the eastern Canadian Arctic: a photographic inventory of June 1973 by R. H. Kerbes
Cat. No. CW65/8-35, Price \$3.25

